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EDITOR

ALEXANDER WILLIAM EVANS

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Errata

Page 149, line 18, for "1–3" read "3–5."
Page 149, line 9 from bottom, for "1–3" read "3–5" and for "130" read "164."
Page 149, line 3 from bottom, for "130" read "164."
Page 150, line 6, for "130" read "164."
Page 287, line 15, for "Meriden" read "West Hartford."
Page 361, FIG. 4 should be numbered "5"; FIG. 5 should be numbered "6"; and FIG. 6 should be numbered "4."
Page 297, lines 16 and 17, omit commas; line 8 from bottom, omit first comma.
Page 310, line 7 from bottom, for "prairie coast" read "coast prairie."
Page 368, lines 24 and 29, for "mm." read "μ."
Page 446, line 4 from bottom, for "*parviflora*" read "*parvifolia*."
Page 452, line 16 from bottom, for "*latifolia*" read "*lateriflora*."

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OF THE

TORREY BOTANICAL CLUB

JANUARY, 1920

Observations on monosporangial discs in the genus Liagora

MARSHALL A. HOWE

(WITH PLATE I AND FIVE TEXT-FIGURES)

The genus *Liagora* is a group of marine red algae of the family Nemalionaceae (Helminthocladiaceae). The species are confined to the warmer seas, where they show a preference for water that is normally agitated, ranging, however, from between the tide-lines on surf-beaten rocks down to a depth of at least one hundred feet. In the West Indian region, including Bermuda and southern Florida, the genus is represented by nine or ten species and one species is known to occur on the Californian coast. With the exception of one species, recently described from Bermuda by Collins & Hervey,* and one from the Mediterranean Sea, the plant body is more or less calcified, the amount of the lime and the way in which it is deposited being more or less characteristic of the various species. Under the compound microscope the thallus is seen to be of an obviously filamentous structure, both the structure and the often lubricous character of the plants when living sometimes calling to mind their fresh-water relatives of the genus *Batrachospermum*.

Most of the species of *Liagora* are consistently dioicous, others are consistently monoicous—characters that hitherto have been rarely ascertained or mentioned in the describing of species, probably because the antheridia are in some species very inconspicuous. The plants rarely seem to be sterile. Antheridia,

* Proc. Am. Acad. **53**: 100. 1917.

[The BULLETIN for December (**46**: 461–502. *pl. 19*) was issued December 31, 1919.]

procarps, or the subsequent cystocarps may nearly always be found, but the writer in examining some hundreds of specimens, has never seen anything that could be certainly interpreted as tetrasporangia or as a non-sexual alternating generation. In the older systematic works, it is either expressly stated that tetraspores in the genus *Liagora* are unknown or else silence is maintained on this point. In Schmitz's treatment of the genus in Engler & Prantl, Die natürlichen Pflanzenfamilien, we find, "Sporangien ungenügend bekannt, angeblich an knotig verdickten Stellen der oberen Thalluszweige aus den Endzellen der Rindfäden entwickelt und unregelmässig paarig geteilt." De-Toni, in his Sylloge Algarum, appears to have carried this statement over into Latin, omitting, however, to translate the "angeblich." Whether this statement by Schmitz rests upon his own personal observations or is based upon some previously published observation that has escaped the attention of the present writer is not clear. Oltmanns, in his Morphologie und Biologie der Algen, is apparently silent in regard to this matter.

In Kützing's Tabulae Phycologicae (8: 43. *pl. 90 I.* 1858) we find in his delineations of *Liagora Turneri* from the Red Sea a figure showing "Ein Gliederfaden, dessen eine Zelle sich zu einer Brutzelle erweitert, aus welcher sich die in *d. e. f. g. h. i.* dargestellten Knospen entwickeln, welche der Anfang der Seitensprossen sind." Structures evidently similar to those figured by Kützing occur in at least four of the West Indian species of *Liagora* (*L. ceranoides*, *L. valida*, *L. farinosa*, and *L. pinnata*), which often show small flat orbicular discs lying on the general surface of the plant or somewhat immersed among the assimilatory filaments. These discs are of a deeper red color than the main *Liagora* plant, they send down few or numerous roothairs from their ventral (proximal) surface in among the assimilatory filaments, and they bear on their dorsal (distal) surface a few sporangia, the contents of which remain undivided, so that they may referred to as monosporangia. Long, colorless, gelatinizing hairs may usually be seen, arising from this outer or dorsal surface. The disc is involved in mucus, the outer limits of which may be distinct or may be vague or imperceptible. Except in the youngest parts of the *Liagora*, this mucous envelope is more or less calcified. These

monosporangium-bearing discs look at first sight very much like independent epi-endophytes. Their darker red color, their dorso-ventral rather than radial symmetry, and the lack of any obvious genetic continuity with the *Liagora* give plausibility to the very natural first impression that they are independent organisms or perhaps obligate epiphytes of various species of the genus *Liagora*. Another plausible *a priori* hypothesis would be that they result from the germination of carpospores and represent a non-sexual alternating phase in the life-history of the *Liagora*. But in support of this latter hypothesis, the present writer finds no direct evidence at all, and the fact that in *L. farinosa* these monosporangial discs are commonly more abundant on antheridial than on cystocarpic plants would seem to point to its improbability. The truth seems to be that these discs arise from gonidia, gemmae, or aplanospores, derived from the terminal or subterminal cells of the assimilatory filaments of the *Liagora*, as was the view of Kützing in regard to similar structures in *Liagora Turneri*. Kützing appears to be the only one who has previously alluded to these structures in print and his observations appear to have been overlooked or ignored by subsequent writers on the genus. These monosporangial discs are especially common in West Indian specimens of *Liagora ceranoides* Lamour. (*L. pulverulenta* Ag.) and *L. farinosa* Lamour. (*L. elongata* Zan.), occurring on both antheridial and cystocarpic plants. In *L. ceranoides*, the gemmae are unicellular or bicellular, terminal or subterminal, solitary or concatenate, but are most frequently derived from the terminal (distal) cells of the assimilatory filaments. The cell enlarges, its contents become deeper red, its walls become soft and mucous, and a new cell wall is laid down inside the old one (FIGS. 1 and 2). Sometimes the rejuvenated cell or aplanospore escapes from the old wall before germinating, but nearly always in this species, as in *L. valida* Harv., germination takes place, or at least begins, *in situ*. The original wall, however, becomes so tenuous that the aplanospore or young disc is very easily detached from its place of origin and even when it develops in its original position, the original walls dissolve so completely that it is usually very difficult to assure one's self of its genetic connection with the filament from which it was derived. Occasionally, the cell, with its original

wall is abjointed as a one-celled gemma, but when abjointing occurs the subjacent cell commonly goes with it, the two together (FIGS. 7 and 8) constituting a two-celled gemma. In this case, the lower of the two cells seems not to divide but to persist as a finally inconspicuous stalk or appendage of the young disc, which results from divisions of the upper cell (FIG. 22). Very rarely (FIG. 28), one finds an irregular pluricellular gemma formed without obvious rejuvenescence or with rejuvenescence limited to one or two of its cells. Occasionally (FIG. 9) several consecutive

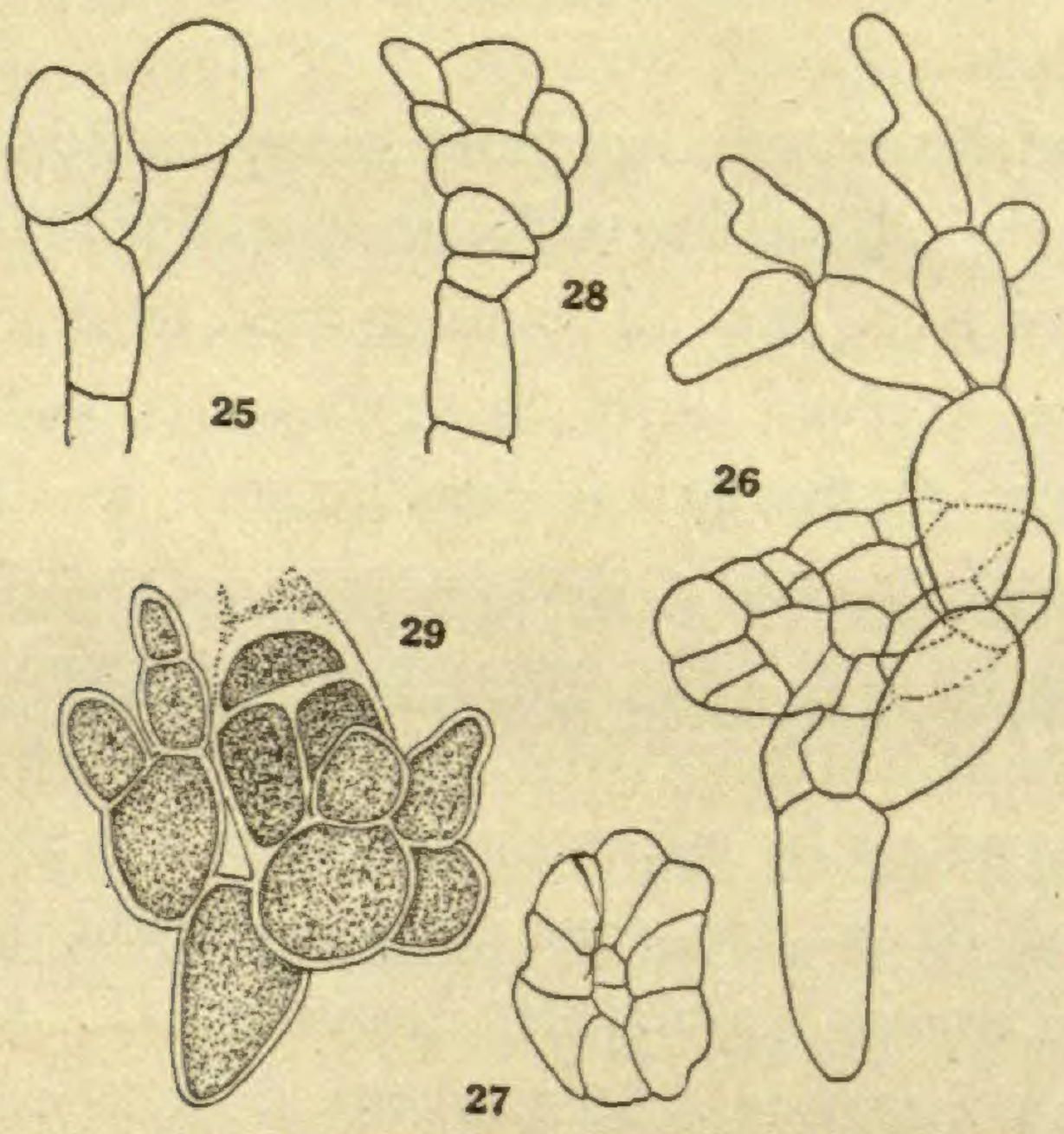

FIG. 25. Terminal cells of an assimilatory filament of *Liagora ceranoides* (No *4778d*, from Montego Bay, Jamaica), showing enlargement and rounding of two of them preparatory to their division to form multicellular gemmae, which develop into monosporangium-bearing discs. × 510.

FIG. 26. A later stage, showing young disc, still attached, disc and stalk-cell together corresponding to a twice forked vegetative branch four cells long (No. *4778d*), × 620.

FIG. 27. Dorsal view of a young disc, slightly smaller than that shown in FIG. 26 (No. *4778d*). × 260.

FIG. 28. Apex of an assimilarity filament showing irregular division to form a gemma (No. *3141*, *L. ceranoides*, Gun Cay, Bahama Islands). × 620.

FIG. 29. A gemma in a three-celled stage, the original mother-cell wall gelatinizing at apex (No. *3141*). × 510.

cells of a filament are converted into aplanospores with evident rejuvenescence and with gelatinization of the original walls. The first divisions of the rejuvenated cell appear to occur in a variety of ways. Often (FIGS. 8 and 29) they suggest the "cru-

ciate" or tripartite divisions of a tetrasporangium and structures of this character may have been responsible for the current somewhat vague and uncertain allusions to the existence of tetraspores in the genus *Liagora*. Occasionally the arrangement of the first segments of the young disc suggests that of the carpels of an orange, sometimes in apparent contravention of the usual rule that a cell divides in a plane perpendicular to its longest axis. When the young disc develops to a manifestly flattened form while still in its original orientation to the parent filament, it is seen (FIGS. 3, 4, and 6) that one of its edges is directed towards the filament, while the first root-hairs (FIGS. 5 and 22), ventral and central as regards the disc, are lateral in respect to the filament.

In *Liagora farinosa* Lamour. and *L. pinnata* Harv., the genetic connection of these discs with the *Liagora* is even more difficult to trace than in *L. ceranoides* and *L. valida*, owing, apparently, to the fact that the aplanospores are released from the more rigid mother-cell walls before germination, so that they do not germinate *in situ*. Hyaline, apparently unicellular hairs, usually several times as long as the diameter of the disc, arise from the dorsal surface and are probably always normally present in younger conditions at least, but owing to their delicacy and to their apparent readiness to dissolve into mucus, they are not always visible, especially in *L. ceranoides*, and they are not represented in our figures (FIGS. 6 and 18) of the disc in this species. The mature discs are suborbicular and are more or less similar in the four species of *Liagora* in which they have thus far been observed by the present writer, yet they show differences corresponding to the peculiarities of the species of which they constitute a part. In *L. ceranoides* and *L. valida*, the discs are softer, more mucous, and less compact than in *L. farinosa* and *L. pinnata*, in which the cells of the disc, like those of the assimilatory filaments of the main plant, have firmer, more rigid walls. In *L. valida*, the discs are thickened in the central part and often radiately unistratose towards the margins, while in *L. ceranoides* the discs give the impression of consisting of more than one layer of cells throughout. Fertile discs are mostly 90–230 μ broad (not including the mucous envelope), though in *L. farinosa*, the plants of which are commonly

the largest of the four species named, they may occasionally reach a diameter of nearly 400 μ. The monosporangia are ellipsoid, ovoid, or obovoid, and are usually 13–26 μ long and 13–18 μ broad, measuring protoplasts only. To what these monosporangia give rise on germination has not been determined but there seems to be some ground for believing that they produce monosporangial discs like those from which they sprang. Species of *Liagora* offer a favorable matrix for the germination of various filamentous algae, including species of *Acrochaetium*, *Ceramium*, and other Rhodophyceae, and inferences that young sporelings associated with a *Liagora* represent stages in development of the *Liagora* itself demand rigorous confirmation, such as might be supplied by cultures or by the presence of a complete series of developmental stages. In this connection, however, it may be remarked that the almost constant association of *Acrochaetium*-like forms with various species of *Liagora* is a suspicious circumstance that deserves further investigation.

In offering the above explanation of the origin of the peculiar monosporangium-bearing discs of certain species of *Liagora*, the writer realizes that he may be charged with having mistaken accidental contact for organic continuity. It would be easier, more conventional, and (*a priori*) more probable to regard the discs as independent or obligate epi-endophytes. Early in his acquaintance with them, the writer was at one time on the point of describing them as representing a new genus of uncertain family, but was deterred by observing that the character of the discs, particularly of their cells and cell walls varied according to the species on which they occurred, and that the discs were progressively older from base to apex of the *Liagora* thallus, the early stages being found only at the extreme apices. The chromatophores, too, seemed similar, except that those of the discs were more red than those of the vegetative cells of the *Liagora*, often as red as those of the carpospores. After much searching, indications that the discs could be traced back to certain cells of the *Liagora* thallus were observed, as shown in the accompanying figures. These observed evidences of direct continuity were not so numerous as the writer might wish and he knows of no analogy among other Rhodophyceae for the state of things here

alleged to occur in *Liagora*. However, he believes the above explanation of the origin of the discs to be correct and ventures to publish his observations in the hope that some one more favorably situated, perhaps with access to living material, with facilities for cultural experiments, and with a taste for cytological investigations, may be able to confirm or disprove them. The possibility that the discs represent an obligate epi-endophyte with a boring parasitic spore deserves special consideration.

THE NEW YORK BOTANICAL GARDEN

Explanation of plate 1

The material from which the drawings on this plate were made was obtained from four species of *Liagora*, all collected by the writer at Montego Bay, Jamaica.

1. Terminal cells of an assimilatory filament of *Liagora ceranoides* (No. *4778d*), showing enlargement and rounding of two cells preparatory to their division to form discs. × 620. (The relations of the branches have been somewhat disturbed and distorted by manipulation)

2. Enlarged terminal cell of an assimilatory filament of *L. ceranoides* (No. *5034*), showing gelatinization of apical portion of wall of original cell and formation of new wall for the rejuvenated cell. × 620.

3. A young few-celled disc of *L. valida* (No. *4778c*), still connected by mucus with the filament from the terminal cell of which it has apparently originated. × 375.

4. A young disc of similar size but with more numerous and smaller cells, the disc probably representing a branch of the filament against which it lies (No. *4778c*—*L. valida*). × 375.

5. A young disc showing its first root-hair and connected by mucus with the filament from the terminal cell of which it was apparently derived (No. *4778c*—*L. valida*). × 375.

6. A young disc in *L. ceranoides* (No. *5034*), with a mucus connection with the end of the filament from the terminal cell of which it was apparently derived. × 375.

7. A two-celled gemma in *L. ceranoides* (No. *4778d*) about to be abjointed. × 620

8. A later stage in the development of a similar gemma after detachment, the distal cell now divided into three cells and the proximal cell remaining undivided, forming a sort of stalk to the young disc (*L. ceranoides*, No. *4778d*). × 620.

9. The terminal portion of an assimilatory filament of *L. ceranoides* (No. *4778d*), showing the formation of several unicellular gemmae or aplanespores in a more or less concatenate series. × 510.

10. A supposed free aplanospore or unicellular gemma before its first division (*L. ceranoides*, No. *4778d*). Possibly, however, a spore from a monosporangium of a matured disc. × 510.

11. A young five-celled disc in which all of the divisions appear to have been lengthwise of the mother-cell, with the first root-hair originating from near one of the poles (No. *4778d*). × 510.

12. A young four-celled disc in which the first division appears to have been lengthwise of the mother cell, followed by the transverse division of one of the daughter-cells (No. *4778d*). × 510.

13. A later stage in the development of a disc, but showing a shorter root-hair (No. *4778d*). × 620.

14. An older stage, with long root-hair and with suggestion of a short stalk at one edge, indicating origin of the disc from a two-celled gemma as shown in Figures 7 and 8 (No. *4778d*). × 272.

15. Dorsal view of a young disc, suggesting discs of species of *Erythrotrichia* and *Erythrocladia* but apparently belonging in the present series (*L. valida*, No. *4778c*). × 510.

16. A later saucer-shaped stage, seen more or less edgewise, and showing three hairs springing from the dorsal surface in its thicker central part and one root-hair from its ventral surface (*L. valida*, No. *4778c*). × 272.

17. Dorsal view of a nearly mature disc with two monosporangia. The dorsal hairs have deliquesced or are so very inconspicuous that no attempt has been made to represent them. The dotted outer line indicates boundaries of the peripheral mucus or gelatinized outer walls. (*L. valida*, No. *4778c*). × 350.

18. An obliquely dorsal view of a mature disc with several monosporangia (*L. ceranoides*, No. *4778d*—edges of disc less monostromatic than in *L. valida*). × 272.

19. Escape of aplanospore from terminal cell of assimilatory filament of *L. farinosa* (No. *4775*). × 375.

20. A free aplanospore from the same plant (No. *4775*). × 375.

21. A young disc of *L. farinosa* (No. *4775*) in ventral view, showing first root-hair. × 620.

22. Another young disc in obliquely ventral view (No. *4775*), showing base of first hair from dorsal surface and first root-hair. × 620.

23. A mature or nearly mature disc of *L. farinosa* (No. *4775*), in lateral view, showing the more or less protuberant monosporangia. The dotted line indicates the boundary of the mucus envelope, which, in the natural state, is lightly permeated with lime. Only about one third of the length of the dorsal hairs is shown. × 272.

24. Obliquely dorsal view of a mature or nearly mature disc of *L. pinnata* (No. *4776*), with monosporangia, etc. × 272.

Studies in the conjugation of Spirogyra ternata

MABEL L. MERRIMAN

(WITH THREE TEXT FIGURES)

The discovery of but four chromosomes in *Spirogyra ternata* led to the collection of material in fruiting condition during the months of October and November, 1915 and 1916. The alga was growing under more or less unnatural conditions in a basin where the water was drawn off during the winter months. Its continued propagation seems uncertain as no trace of it was found in the fall of 1917 or 1918.

The large size of the nuclei, the low number of chromosomes, the few chromatophores, and the general transparency of the cells, combined with marked sexual differentiation of the filaments in conjugating periods, are features that make this species especially favorable material for the investigation of such debated questions as the potential bisexuality of vegetative cells, chromosome reduction, and the history of the secondary nuclei in the sporophyte generation. While material was at first studied with the hope of elucidation of these problems, continued study of the filaments brought to light interesting changes in the cells as they pass from the vegetative condition to a state of conjugation.

The diagnostic features of *S. ternata* Ripart (1876), as described by Collins (2, p. 114), are as follows: filaments 50–65 μ in diameter, with cells 1½–2 diameters long, somewhat swollen at the middle; zygospores ovoid, 45–66 μ in diameter, 1–1½ diameters long.

The form collected in 1915 varied from this in having its vegetative cells 74–80 μ in width. The zygospores in this 1915 material measured 64 μ in width and 120 μ in length. In the 1916 material there was much greater variability and frequent hybridization with a larger species resembling *S. jugalis* but differing in the shape of the fertile cell. The comparison of *S. ternata* with another species, *S. maxima*, growing under the same conditions and fruiting at the same season, revealed such great

differences in the form of the conjugating tubes and cell contents as to suggest the problems investigated in this paper.

A sinuosity is to be noted in the filaments in both vegetative and fruiting states, associated with a certain degree of motility. It is questionable which is the greater contributory factor to these movements, inequalities of growth or inequalities in the turgor of the cells, increased possibly by the mucilaginous layer on the cell wall. When in a state of conjugation the short portions of threads of *S. maxima* which are contained in the field of view under the low power of the compound microscope can be seen to be straight and to consist of large cells joined by small and narrow tubes. The fertile cells of this species are always unswollen. In *S. ternata* straight threads are rarely to be seen and then only in the earliest stages of conjugation, while a marked feature of the species is found in the swollen ♀ cells. The swelling often affects the cells throughout their entire length and sometimes increases their volume twofold, if the extensions of the conjugating tubes are taken into account. The filaments of *S. ternata* not only show a notable sinuosity, but in the curvatures of the filaments the two sexes always have a definite relation to each other, in spite of the fact that there are certain irregularities in the number of the cells. A comparison of numerous threads, whether lying in water or preserving fluids, showed that the filaments always assumed curves which varied from those slightly bent to those forming semicircles. Further examination disclosed the fact that the ♀ threads were invariably lying on the outer side of the curve, unless displaced or twisted in mounting. Often, in the water, the conjugating threads would naturally twist, but in so doing the ♀ thread, after a turn of a few cells, would again be found lying outside the ♂ filament.

S. ternata is an example of typical scalariform conjugation, for in the hundreds of filaments studied the movement in the conjugating cells was always found to be in one direction. It would be of interest to discover cases of cross conjugation, such as those reported by Cunningham (3) in a smaller species of *Spirogyra*. If forms of cross conjugation should be found, where regular alternating movements of contents take place, cells with straight outlines would seem probable, while if threads were found

containing several cells of one sex and then several cells of the opposite sex a zigzag position of the threads might be expected, instead of the symmetrical curves found in such a typically dioecious form as *S. ternata*.

It would seem that a continuous movement of contents of the ♂ cells in one direction, thereby increasing the contents of the ♀ thread as the zygospores form and subjecting it to a greater geotropic stimulus, would cause a sagging of the thread, resulting in its taking an outer or lower position in reference to the ♂ filament. Yet, in the majority of cases where the curvature was extreme and where the ♀ thread uniformly kept its position, there had been no appreciable movement of the contents, even when a complete formation of the conjugating tubes had taken place. This was evidenced by the fact that the chromatophores were unrelaxed in position and also by the intact connecting walls of the conjugating tubes. Since a large amount of conjugating material was available it seemed desirable to scrutinize more closely this relation of filaments in conjugation. It seemed possible that the degree of curvature might be dependent upon the amount of tumidity of the cells and not upon the degree of advancement in the formation of the zygospores. It was hoped also to bring to light more information as to the number and nature of the sexually potent cells and the manner of formation of the conjugating tubes.

Camera drawings were made of many pairs of filaments, in some cases numbering over fifty cells. A magnification of 140 diameters was used in order to have as many cells as possible in the field of view and yet to see clearly the position of the nuclei and chromatophores. Measurements of the drawings for length of the cells and filaments were obtained by two methods. In the first method a piece of thread held without undue tension, following the curving outer walls of the cells, was measured with the metric ruler. Slight discrepancies in this method would be due to the varying tension of the measuring thread. The other method employed, when it was desired to compare cell with cell instead of filaments as a whole, was to measure the distance from one transverse wall to the next with the ruler, not allowing for the convexity of the lateral walls. Such distances added would bring

out changes in the length of the filament as a whole but would not take into account differences in the two sides of the cell and in the extent of the cell walls.

For the ascertaining of these relations the two sides of the cell in each sex were measured in some of the most curved examples. The distance between the ends of the transverse walls opposite to the conjugating tube was taken in each case for measurement, as the various degrees of bulging of the inner walls where the tube emerged made accuracy difficult. When accurate measurements were needed to determine the size and position of the various cell organs, such as the nuclei and pyrenoids, higher powers and the ocular micrometer were used. Measurements of the drawings by means of the thread following the curving lateral walls always gave figures in excess of the sum of the lengths of the cells measured individually. Both of these methods, when so many hundreds of cells were examined, involved far less labor than the use of the ocular micrometer and gave the same relative proportions in the lengths of the cells.

The various measurements obtained in each series of observations have been arranged in tables. If a longitudinal series of cells is considered an individual plant, only a portion of a plant was measured in each case. It would, in fact, be impossible to be sure in collecting material that an entire thread, resulting from the germination of a zygospore, had been obtained. In this work, however, the cells of the *Spirogyra* have all been held as potentially the same.

Series A (FIG. 1) represents a pair of threads chosen for study by reason of their great convexity and torsion. In this series none of the opposing cells had apparently mingled their contents, and the nuclei are to be seen in their central positions with the chromatophores unrelaxed and contiguous to the cell wall, as in ordinary vegetative cells. In mounting these threads in the liquid on the slide the curvatures between *A* and *B* and between *C* and *D* in the figure projected much above the surface. Though a cover-glass was carefully lowered upon them the torsion was such that the flattening of the surface caused a breaking of the ♂ thread of the pair at *D*, one of the most curved points. Camera drawings were made of the threads as they were thus mounted,

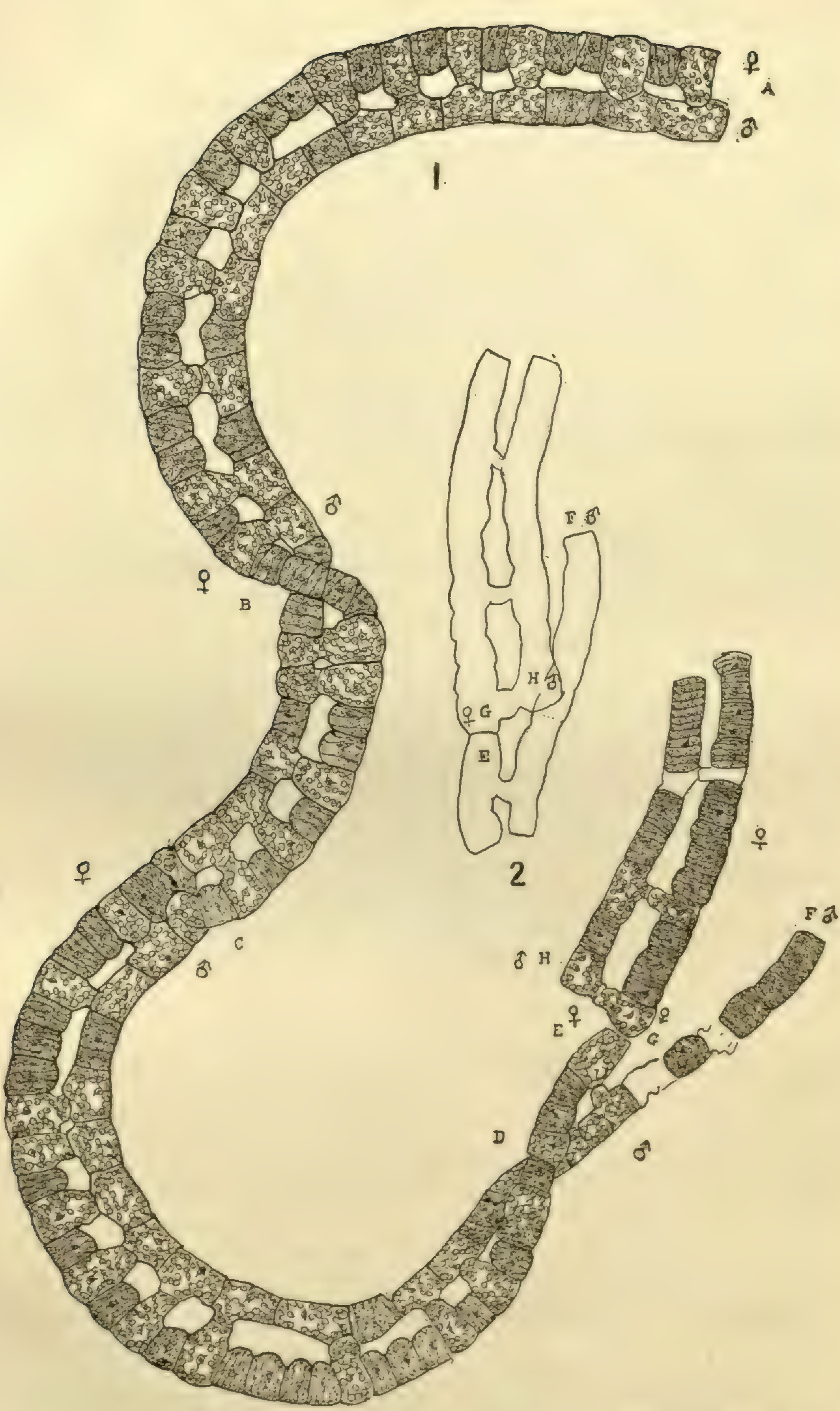

FIG. 1. A pair of conjugating filaments, showing torsion at points *B*, *C* and *D*; the ♂ thread is broken at *F*. × 140, reduced one half.

FIG. 2. A model of the broken filament replaced in its original position, showing relaxation in ♂ cells thatwere previously compressed.

the broken portion (upon lowering the coverglass) being reversed from its original position. FIG. 1 shows these threads as drawn originally, while FIG. 2, made by reversing a model of the broken threads, shows them as they were in their first position except for the break. The rupture of the thread reveals the previous tension of the cells. Upon severing the ♀ thread at *G* and then placing the terminal cell *H* of the ♂ thread next to the cell *F* from which it was broken, the ♀ thread, by reason of the relaxation of the ♂ cells in the breaking of the thread, lacks 45 mm. of meeting the cell *E* in the figure. When, on the contrary, the cell *G* is placed next to *E*, as in the model of the reversed cells, the thread shows a marked linear extension, indicated by the distance from *F* to *H*, the point to which *F* was previously joined. When this extension is measured by adding the distances between transverse

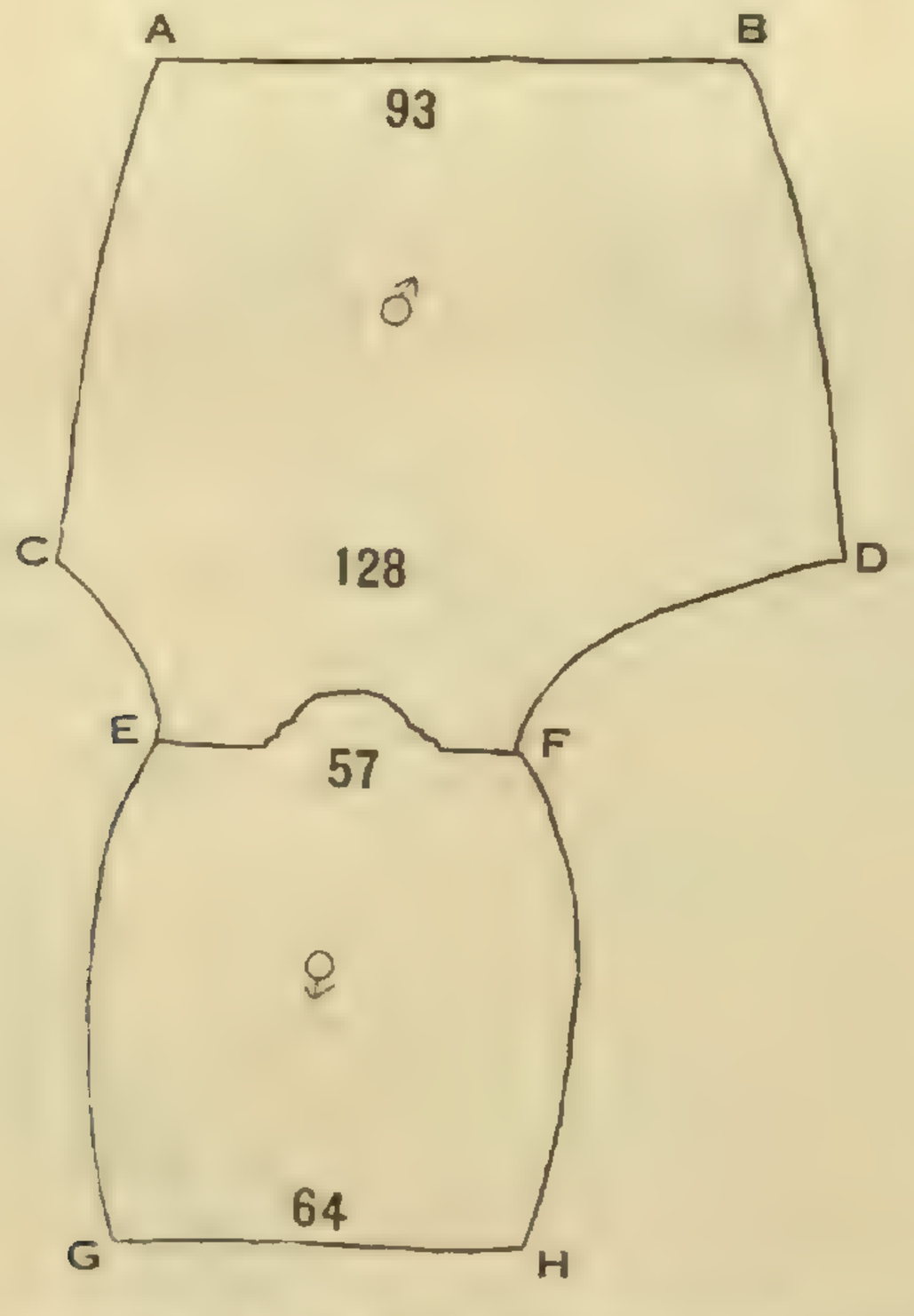

FIG. 3. Diagram of conjugating cells, illustrating distances between transverse walls as measured with the ocular micrometer.

walls it gives an excess of 43 mm.; when measured by a thread allowing for the curving walls, it gives an excess of 55 mm. These figures are an index of the amount of compression of the ♂ thread at this region of curvature.

The ♀ thread in this curved series, as shown in TABLE I, consists of ninety-five cells; thirty-six of these are conjugating

cells with their tubes formed, an equal number show by their tumidity an approach to the conjugating state, while only twenty-three show no signs of conjugation. Since there are only fifty-six cells all told in the ♂ thread it is obvious that many of the tumid ♀ cells would have proceeded to abortive conjugation. In the two portions of the filaments, *A–B* and *C–D*, where the curves are greatest and where in consequence the ♂ thread is under the greatest compression, it should be noted that the ♀ cells which show tumidity are opposite ♂ cells which have already conjugated. Seven conjugating cells in succession are included in the semicircular curve *C–D*, while in the curve *A–B* there is a succession of

TABLE I

SERIES A

Sex	Number of cells	Length of drawing of magnified filaments in mm. measured by thread	Sum of magnified lengths of cells, measured with ruler	Conjugating cells		Cells tumid, conjugating tubes not formed		Non-conjugating cells		Ratios	
				Number	Average length, microns	Number	Average length, microns	Number	Average length, microns	Potent cells (incl. tumid)	Non-potent
♀	95	779	701	36	63	36	48	23	42	.757	.242
♂	56	612	603	36	84	4	62	16	65	.714	.285
Excess.....	♀ 39	♀ 167	♀ 98		♂ 21	♀ 32	♂ 14	♀ 7	♂ 23	♀ .043	♂ .043

twelve conjugating or tumid cells with a single interruption. It is to be noted that the compression in the ♂ filament occurs before the rupture of the tubes and the mingling of the cell contents and hence before the relaxation of the chromatophores. In TABLE II the cells of Series A are grouped according to the length of the outer walls.

The next measurements taken were those of the distances between the outer and inner terminal points of the transverse

TABLE II

CELLS OF SERIES A ARRANGED ACCORDING TO LENGTH OF OUTER WALL

Length outer wall in microns	101–108	94–101	87–94	80–87	73–80	66–73	59–66	52–59	45–52	38–45	31–38	24–31	17–24
♀ conjugating.....			1		1	14	9	5	3	1	2		
♂ conjugating.....	2	6	4	5	14	2	2				1		
♀ tumid.....							2	10	10	7	6		1
♂ tumid.....					2	1				1			
♀ non-potent.....								3	7	7	3	2	1
♂ non-potent.....					4	3	3	3	2	1			

walls in each sexual cell. The significance of these measurements can be seen more clearly by taking as an illustration a single pair of cells, as in the accompanying FIG. 1. A ♂ cell, *ABCD*, has an outer wall, *AB*, measuring in a straight line 93 μ between the points *A* and *B*, this distance being less by 35 μ than a similar measurement in a straight line between the points *C* and *D* of the inner wall, from which the conjugating tube emerges. If the walls were originally an equal distance apart, as is the case in filaments where all the cells are non-conjugating and where external conditions are such as to cause no marked inequalities of growth in the two sides of the cells, *A* and *B* of the ♂ cell are brought nearer together, as conjugation proceeds, while *C* and *D* are spread farther apart. Internal pressure, the result of the metabolic activities of the protoplast, must cause this distension of *CD*. In the ♀ cell there is either no change whatever in the distance of *G* from *H* or only a slight increase. A study of the

TABLE III

CELLS A—B INCLUSIVE

LENGTHS GIVEN IN MICRONS

Number of ♀ cell	Length outer wall	Length inner wall	Outer wall increase	Conjugating with	Number of ♂ cell	Length outer wall	Length inner wall	Outer wall decrease
1	64	61	3	⟷	1	107	114	− 7
2	50	50	0					
3	71	71	0	⟷	2	100	96	+ 4
4	43	43	0		3	82	86	− 4
5	53	50	3					
6	64	64	0	⟷	4	79	89	−10
7	43	36	7					
8	57	50	7	⟷	5	79	79	0
9	61	57	4					
10	57	57	0	⟷	6	79	86	− 7
11	50	50	0					
12	71	64	7	⟷	7	71	86	−15
13	57	57	0		8	64	71	− 7
14	50	50	0					
15	64	64	0	⟷	9	71	86	−15
16	64	57	7					
17	79	57	22	⟷	10	107	129	−22
18	50	50	0					
19	79	71	8	⟷	11	100	107	− 7
20	64	64	0					
21	61	50	11		12	50	71	−21
22	79	71	8	⟷	13	86	100	−14
23	64	50	14		14	79	79	0
24	64	57	7		15	79	100	−21
25	71	71	0					
26	43	36	7					

membranes joining the completely formed conjugating tubes shows that the center of the tube pushes against the wall, forming a secondary smaller tube shown in the diagram. Probably it is the stretching of the wall as this tube presses against the wall of the cell that brings *E* and *F* nearer together.

Inspection of the TABLES III and IV, representing measurements of the cells where the curves in the filaments were greatest,

TABLE IV

CELLS C—D INCLUSIVE

LENGTHS GIVEN IN MICRONS

Number of ♀ cell	Length outer wall	Length inner wall	Outer wall increase	Conjugating with	Number of ♂ cell	Length outer wall	Length inner wall	Outer wall decrease
1	61	50	11	⟷	1	86	100	−14
2	43	36	7		2	79	100	−21
3	57	50	7					
4	64	50	14					
5	71	71	0	⟷	3	79	100	−21
6	57	57	0	⟷	4	79	86	− 7
7	43	43	0					
8	71	64	7	⟷	5	100	114	−14
9	50	50	0					
10	64	64	0	⟷	6	71	79	− 8
11	57	50	7					
12	64	57	7	⟷	7	93	107	−14
13	57	43	14					
14	71	64	7	⟷	8	100	107	− 7
15	50	43	7					
16	57	57	0					
17	42	42	0					
18	57	28	29					
19	57	50	7	⟷	9	111	128	−17
20	35	35	0		10	50	86	−36
21	50	50	0					

A—*B* and *C*—*D* inclusive, show the opposing numerical relations between the outer and inner walls of the two series.

From the comparison of the increases and decreases in the lengths of the walls in the two filaments a marked tendency is apparent toward lengthening the inner distance between the transverse walls of the ♂ cells, the corresponding distance between the transverse walls of the ♀ cells remaining the same or showing a slight decrease. The changes in length are brought about just before and during the process of conjugation. There is no reduction to be seen in any of the outer walls of the ♀ cells in these series, their excess lengths varying from zero up to 22 μ. In the case of the seventeenth cell, where there is the unusual in-

crease of 22 μ, the corresponding cell of the ♂ filament shows a reduction of 22 μ in the outer wall. This equality is presumably a coincidence, since the second ♂ cell in TABLE IV shows a similar reduction of 21 μ in the outer wall. This cell is not conjugating but is opposite tumid cells of the ♀ thread and is probably influenced by them.

In the ♂ filament there is a reduction in the outer wall in every cell but the second from the end *A*. In this cell it is to be seen that more of the wall than is usually the case takes part in the formation of the tube. All of this wall is elevated from the level of a straight line connecting the transverse walls. The bulging of this wall has probably counteracted the usual tendency of the inner parts of the transverse walls to spread apart.

According to these measurements, then, the compression in the filament, as revealed in the breaking and subsequent replacement of the broken parts, does not involve the filaments as a whole but is restricted in its extent to the parts of the cells which are farthest from the conjugating tube. Measurements also indicate that differences in tension in the ♀ cells are not so different from those occurring in vegetative cells. In this connection it is to be remembered that all the cells of a filament are in a state of slight compression, for when a filament is broken or an intervening cell dies the end cell extends slightly, rounding off and assuming the regular shape of an ordinary terminal cell. This does not explain the striking and opposing differences in tension found exclusively in cells in the conjugating state.

In another part of this investigation other changes in the conjugating cells will be considered, especially the formation of the tubes. There it will be noted that more of the inner wall of the ♀ cell takes part in the formation of the tube than is the case with the ♂ cell. Hence, as in FIG. 3, where *E* and *F* of the ♀ cell are always nearer relatively than *C* and *D* of the ♂ cell, the linear extension of the conjugating tube of the ♀ cell will be found to exceed that of the ♂ cell, if all of the linear extension pressing against the opposing wall is considered. However, it is the bringing together of the transverse walls and the consequent rectilinear contraction of one side of the filament at the beginning of conjugation that results in the constant relative positive of the

two sexes. This relative position was even maintained when *S. ternata* conjugated with the much larger species present. Whether a large ♀ cell of this species united with a small ♂ cell of *S. ternata* (the two differing by 32–50 μ in cell width), or whether a large ♂ cell conjugated with a smaller ♀ cell of *S. ternata*, this same relative position of sexes was maintained. The ♀ thread, whether larger or smaller, was always seen to occupy the outer position in the curve.

Studies will be presented also of the curvatures maintained in cases of triple and quadruple combinations of threads. Many examples were studied where one ♂ filament is conjugating with two ♀ filaments and, reciprocally, where one ♀ filament is conjugating with two ♂ filaments. Frequently a ♀ cell was found conjugating successfully with a ♂ cell on one side while the ♂ cell on the other side, though the conjugating tube had formed, showed only abortive conjugating. In the case of such an abortively conjugating cell it is important to note that the constant and marked inequalities in the distances of the transverse walls, seen in normally conjugating ♂ cells, were never exhibited. Except for its projecting tube the abortively conjugating ♂ cell, in the measurements between its transverse walls, accords more with those of the of the normally conjugating ♀ cell than with those of the normally conjugating ♂ cell. Abortive conjugation in *Spirogyra* has been previously reported by Bessey (1), Robertson (5) and, more recently, by Cunningham (3).

The work of Riddle (4) on the nature of sex in pigeons has a suggestive bearing upon these observations made on conjugating *Spirogyra*. He states, as a result of his extensive experiments, that sexual differentiation is to be interpreted as the expression of quantitative differences in the rate of protoplasmic activities, the more active metabolism resulting in males. With a low level of metabolism in the female is associated large size of yolk, low percentage of water in the yolk, high percentage of stored material, and a high total of stored energy. His review of the literature shows evidence of a relation between the rate of metabolism and sex in a great variety of animals, ranging from worms to man. Although his work and conclusions relate only to the animal kingdom he makes the conjecture that it would be of interest to

determine whether in dioecious plants there is a corresponding difference in the rate of metabolic exchange.

Since the ♂ gamete of *Spirogyra*, in contrast to the spermatozoön of animals, carries with it to the receiving gamete stored food as accretions about the pyrenoids, a high percentage of stored material does not occur in the ♀ cell until after conjugation is completed. The large proportion of swollen cells, both with and without conjugating tubes, and the fact that no visible movement of solid parts has as yet begun in the conjugating cells indicate that the different tensions shown by the measurements of the sex cells are to be causally connected with the differing amounts of tumidity and this in turn with different types of metabolism in the sex cells.

It would be premature to draw final conclusions from the intensive study of but one series. The comparison of Series A with other series observed, the tabulation of results and deductions as to potency of cells, formation of tubes and other related problems must be reserved for another paper.

HUNTER COLLEGE, NEW YORK CITY

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Some applications of the quadrat method

HENRY ALLAN GLEASON

By the quadrat method in ecological phytogeography is meant the intensive study of the vegetation or environment of a limited and definitely circumscribed area, known as a quadrat, in order to gain a comprehensive knowledge of the vegetation as a whole. The development of the method is the direct outgrowth of a need which has been felt by every ecologist who has seriously attempted the study of vegetational units. While its use is of great value and leads frequently to generalizations which would otherwise be difficult or impossible, it is not complete in itself, and ecologists are unable to rely upon it alone as a means toward successful field work. Indeed, its use to the exclusion of all other methods has never been suggested. It does constitute, however, the only practicable means for the quantitative study of the association, and as such it forms an important adjunct to photography and verbal description, which were previously the only feasible means of presenting the structure of vegetation. It also plays an important part in the study of associational dynamics, as migration and succession, and environometry.

It is exceedingly difficult and in many cases impossible for a reader to form a clear mental picture of an association from a written description, as may be demonstrated by a perusal of any discussion of an otherwise unfamiliar type of vegetation. The value of a verbal description is always greatly enhanced by photography. There are certain physical limitations to the value of a general photograph, caused by the difficulties of field photography and the necessity of reducing the print to the usual compass of a page, so that a general view of an association seldom gives a sufficiently clear idea of the vegetation, since the component species are distinguishable only in the immediate foreground, if at all. A detailed photograph of a small part of the association, on the other hand, is frequently made with difficulty and it is often impossible to choose for illustration an isolated portion which is

typical of the association as a whole. In the latter case, and in all cases of verbal description, the result unconsciously and unavoidably embodies the author's idea of the conditions, rather than the actual and impersonal facts, in that conspicuous species may be emphasized although possibly relatively unimportant, while important but comparatively inconspicuous species may be neglected. While the quadrat method is by no means a panacea for all these difficulties, its proper combination with verbal description and photography does much to aid the observer in securing a thorough knowledge of the association and in more satisfactorily expressing its structure in terms intelligible to his readers. The merit of the method lies not merely in the actual results which it affords but also in the deductions from and application of these results.

While quadrats may be of any chosen size, a single square meter is probably most frequently used. In the list quadrat, a simple list is prepared of the species included within it. In the count quadrat, the number of individuals of each species is also determined. Both of these are of value as a method, but are of little use in expressing results. For the latter purpose, the map quadrat is by far the most useful. A chart is prepared on a suitable scale, usually 1 to 10, and the location of each individual plant noted upon it. Other sorts of quadrats may be made for special purposes, concerning which reference may be made to the various works by Clements (1904, 1905).

The structure of a vegetational unit depends upon the species represented, determining the flora; on the relative number of individuals of each, determining by their form, size, and habit the appearance of the vegetation; and on the total number of individuals, determining the density of the vegetation.

The use of a chosen quadrat in representing this structure depends absolutely on the theory of the homogeneity of the association, which in turn depends on a number of factors (Gleason, 1917, p. 471). Given a uniform physical environment, the mere migration of some species over the whole area requires considerable time and interferes with the uniformity until it is accomplished, so that young associations are always less uniform than old ones, while in open associations migration may continue for a

very long period. Minor differences in environment may lead to the predominance of certain species in favorable places, to the persistence of relics, or to the early appearance of pioneers of other associations. Uniformity can not be perfect, although the general tendency of vegetation (apart from the effect of disturbing physical factors) is always toward uniformity, and it is most nearly attained in old (climax) closed associations, where entrance of new species is prevented by vegetative control of the environment, or in associations of extreme environment, where a small group of adjusted species enjoy a monopoly of the area.

If the association were absolutely homogeneous, if the plant individuals of the different component species were as regularly distributed as water and alcohol in a mixture of the two liquids, all quadrats of appreciable size would be similar and any quadrat could be chosen to represent the vegetation. Since no association is perfectly uniform, any one quadrat may by its structure accentuate the variability instead of concealing it. The value of a single quadrat also depends on its size and on the number of species in the association. In communities of numerous species (75 or more), a meter quadrat seldom includes as many as fifteen of them and usually contains still fewer. In very open associations, a meter quadrat frequently includes but a single individual plant. In either case, the error is reduced by increasing the size of the quadrat, but this simultaneously increases the labor of charting and decreases the value of a photograph.

The single quadrat of small size, one to two meters square, is therefore essential for graphic illustration, either by photograph or map, and is undoubtedly of value also for experimental work, but it fails to give a fair representation of the whole association, and is of less value as a basis for written description or as a unit for intensive study in field work. To be sure, a suitable quadrat may be chosen, but the quadrat method itself, as ordinarily used, offers no aid in the selection of this typical area, so the actual choice invariably represents the observer's idea rather than the impersonal facts.

The chief value of the quadrat method lies in the results obtained from the study of many quadrats, chosen at random to avoid the personal element, scattered over an area wide enough

to be representative of the whole association, of sufficient number to permit drawing logical conclusions, and of a size suitable to the character of the vegetation concerned. Several ecologists have devised statistical methods toward this end, which have been more or less successful. One of the earliest was Drude (1890), who described plants as social, gregarious, copious, or rare, depending on their number, their distribution, and their grouping. He also proposed the determination of the frequence of plants on a large scale by dividing an area into quadrats of 100 square kilometers. Pound and Clements (1898, 1900) adopted the same terminology in their first studies on the subject, but determined abundance within a single association by actual counts of the number of individuals in a quadrat 5 meters square, and investigated enough quadrats to warrant them in drawing averages. It is obvious, however, that averages from figures obtained in this way are not entirely trustworthy, since some species are mutually exclusive, while the averages might indicate that they normally grew together. Jaccard (1901) adopted the study of several adjacent quadrats as a method in his study of alpine vegetation, and developed the idea of the frequency index and the community coefficient. His results are, however, probably somewhat faulty, inasmuch as he used few quadrats in any one association and located them adjacent to one another. Harper (1917 and several other articles) has also attempted a statistical expression of car-window observations, which corresponds to some extent to the frequency index as here used. Raunkiaer (1909) used essentially the same method described here.

The present writer first attempted the use of statistical methods to determine and express the structure of vegetation in 1903 (1907). He improved his method somewhat in 1908 (1910) and adapted it to class work with students in 1910. In the summer of 1911 he began the intensive study of the quadrat method and its applications at the Biological Station of the University of Michigan, and during the following four summers obtained a long series of data upon which the present paper is based. The statistics used in TABLES I and II were secured from the aspen (*Populus tremuloides* and *P. grandidentata*) association.

In practice, the following method is adopted. The size of the

quadrat to be used is determined first by the general character of the vegetation, using a small one, one square meter, for dense closed vegetation, and a larger one, two meters square, for open or irregular associations. The quadrats may be marked out by four stakes connected by a line of proper length, or they may be estimated by the eye with sufficient accuracy for all practical use. The optimum size can be ascertained after an examination of the preliminary results, and the survey can be repeated with a better size of quadrat if the first is unsatisfactory. The number to be counted depends upon the visible uniformity of the association, on the area covered by it and on the time available. If possible, one hundred are counted.

The first one is located anywhere. The others are located successively in a pre-decided relation to the first, thereby obviating any element of personal choice. Thus they may be in a straight line and separated by ten paces each, so that the whole strip of one hundred would be one kilometer long; or they may be in a square, but similarly separated, so that the area examined would be approximately 100 meters square; or any other arrangement of separate or contiguous quadrats may be used, depending upon the configuration of the association.

For the first quadrat, the species are listed and the figure 1 placed after each in a single vertical row. For the second, the figure 2 is placed after the 1 for all those species which occur also in the second quadrat, and new names followed by the figure 2 are added for the additional species. The process is continued to completion, when it is seen that some of the species occur in a majority of the quadrats and others in a few or only in one, and the common species are distinguished from the rare ones as the work proceeds.

At the conclusion of the count, the results are summarized and the ratio between the total number of quadrats and the number in which a particular species occurs is expressed as a percentage which is known as the *frequency index*, here abbreviated to *FI*. Thus, the frequency index of a common species may be as high as 100 and most associations show certain species with *FI* 90 or more, while others are as low as 1.

Obviously not every species of the association will appear in

the counts. Some of the rarer ones will be missed completely. For example, during five years experience in the aspen association of northern Michigan, during which some thousands of quadrats have been counted by the writer or his students, *Cypripedium acaule*, a plant of great rarity in this habitat, has appeared but once in the quadrats. These rarer ones, while of the greatest interest to the systematist or the phytogeographer in their relation to plant distribution in general, as emphasized so interestingly by Fernald (1919), and to the ecologist through the evidence which they frequently offer concerning the past or future development of the association, are nevertheless of negligible value in formulating a verbal description of the association. But the important species all do occur, provided the number and location of the quadrats has been properly chosen with reference to the size and character of the association, as the writer has demonstrated frequently in his own work.

If the whole association were included in a single quadrat, the frequency index of each species would be 100 and would give no idea of the comparative value of the species. In general, if the quadrats are too large, the frequency indices are also large and tend to approximate near 100. Conversely, if they are too small the indices are also small, and tend to approximate near unity, while the number of omitted species tends to become large and may even include some of the more important ones. The optimum size is one in which there is a wide divergence in the indices, from 1 to 90 or even more, so that the variation is an indication of the relative importance of the species. This is illustrated in the first three columns of figures in TABLE I,* of which the second column, based on quadrats two meters square, presents probably the best series of indices.

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* The frequency indices given in TABLE I are not considered typical of the aspen associationi n general. The association consists of a sparse growth of two species of aspen and the paper birch, alternating with treeless areas dominated by bracken fern. The 240 quadrats counted for this paper were located entirely within a treeless area, and do not take account of the conspicuous difference encountered in the shade, where *Melampyrum lineare* and *Diervilla Lonicera* are both abundant. Neither do they cover an extent wide enough to give a fair representation of the treeless areas in general, since these omit completely such relatively common species as *Vaccinium canadense*, *Panicum depauperatum*, *Oryzopsis pungens*, and *Convolvulus spithamaeus*.

Again, the number of quadrats counted determines the accuracy of the frequency index as an expression of the ecological value of each species. The results from a small series certainly can not express the actual conditions as well as those from a large

TABLE I

	FI in 15 quadrats of 16 square meters	*FI* in 60 quadrats of 4 square meters	*FI* in 240 quadrats of 1 square meter	*FI* in every fourth quadrat	*FI* in first 60 quadrats	*FI* in second 60 quadrats	*FI* in third 60 quadrats	*FI* in fourth 60 quadrats
Pteris aquilina	100	100	99	100	98	100	97	100
Vaccinium pennsylvanicum	100	82	71	70	82	78	97	27
Gaylussacia baccata	80	67	48	43	60	25	87	22
Aster laevis	100	68	29	30	37	30	23	27
Carex umbellata	87	53	24	33	57	20	7	13
Rhus glabra	73	55	23	25	33	15	3	40
Rumex Acetosella	80	40	21	28	7	33	33	12
Rubus allegheniensis	40	30	17	18	37	15	10	7
Panicum boreale	60	35	16	17	5	12	17	32
Danthonia spicata	40	22	15	13	2	48	3	7
Gaultheria procumbens	47	27	14	10	7	20	25	5
Gnaphalium decurrens	60	33	12	15	2	20	17	8
Populus grandidentata	53	32	11	10	0	10	8	25
Hieracium venosum	60	28	8	7	3	7	5	18
Erigeron canadensis	33	20	7	8	5	0	2	22
Panicum xanthophysum	20	13	6	3	0	2	0	23
Diervilla Lonicera	13	8	4	3	15	0	0	0
Solidago canadensis	33	8	2	2	2	0	3	5
Agrostis hyemalis	27	8	2	3	7	2	0	0
Lactuca canadensis	20	7	2	2	3	0	2	2
Poa compressa	13	5	1	2	2	3	0	0
Epigaea repens	20	5	1	0	0	0	3	2
Quercus rubra	13	3	1	3	2	0	2	0
Comandra umbellata	7	2	1	2	0	3	0	0
Amelanchier canadensis	7	2	0	0	0	2	0	0
Hieracium paniculatum	7	2	0	2	0	0	2	0
Pinus resinosa	7	2	0	0	0	0	0	2

series. Repeated tests have shown that 100 is a satisfactory number and that no valuable increase in accuracy is gained by increasing the number beyond that, while it eliminates all computation in determining the frequency index.

Experience has also shown that better results are obtained if the quadrats are not contiguous, but separated by some distance, so as to cover more thoroughly the whole area of the association. In small associations, where even contiguous quadrats cover most of the area, this treatment is not necessary. If plants were

distributed absolutely at random over the association, that is, if the association were absolutely uniform throughout, separated quadrats would never be necessary. But plants are not distributed entirely at random. Each plant-parent gives rise to disseminules which occupy, roughly speaking, a circle about it, with a diameter depending upon the mobility of the disseminules. As early as 1903 the writer (1907, p. 159) was able to demonstrate these in his field work. As a check, the following data from 240 one-meter quadrats are offered. The 27 species have frequency indices ranging from 0 (1 quadrat only) to 99, based upon the whole series. If any fourth part of the series is taken as a basis, composed of 60 contiguous quadrats, as shown in the last four columns of TABLE I, the average discrepancy between the two series of indices is 6.8, or for the 15 commonest species 10.7, and the difference may be as high as 44 for a species which normally grows in patches. But if every fourth quadrat is taken as a basis, that is, 60 separated quadrats, as shown in column 4 of TABLE I, the greatest discrepancy is only 9 and the average only 1.9, or 2.7 for the commonest species. In other words, 60 quadrats well scattered give results practically as reliable as 240 contiguous ones.

From a list of the frequency indices, made from quadrats of suitable size and number, the species are arranged in order of their general distribution in the association, and any number of them may be segregated for further study as the most typical or commonest. Since the frequency index increases with the size of the quadrat, a quadrat of proper size may now be chosen which will normally include all the more important species as well as a number of the less important ones also. The size of this *major quadrat* may be determined in advance and, in field work with students, one of them assigned to each student for detailed study and description. Although every such major quadrat may not actually contain all the important species, the student may be assured that it is nevertheless a fair sample of the association as a whole. The value of setting a definite area before each student, in which he may do his more intensive work, will be at once apparent to every teacher who has tried to present this phase of ecology in the field. The method of determining the major quadrat will be discussed below.

The relative abundance of a species is a fair measure of its ability to maintain itself under the conditions of environment and competition prevalent within the association. Long-established species of an old association have frequently become diffused thoroughly over the whole area, and their abundance may be determined by counting, but recent immigrants into old associations or any species of young associations are not uniformly distributed. The number of individuals of such plants is therefore zero in those parts which they have not yet reached and is too high to show their relative adjustment in those parts which they have reached.

But there is a definite relation between the number of individuals of a species and its frequency index. If only one is present in the area covered by the quadrats, the frequency index naturally cannot exceed 1. If only two are present, it can not exceed 2 and may be only 1 if both happen to occur in the same quadrat. While it is possible for a species to be represented by a large number of individuals all of which occur in a single quadrat only, the chance of such a thing actually happening is very small indeed. Similarly, while 100 individuals might be so thoroughly distributed that they would occur one in each quadrat, there is again very slight probability of it. The mathematical possibilities are capable of solution according to the laws of probability and chance. If n plants are scattered at random over q quadrats, the probability of any one quadrat being occupied is expressed by the formula $1 - \left(1 - \frac{1}{q}\right)^n$. Thus for 2 plants in 5 quadrats $1 - \left(1 - \frac{1}{5}\right)^2 = 0.36 = FI\ 36$. Or for 65 plants in 100 quadrats $1 - \left(1 - \frac{1}{100}\right)^{6/5} = FI\ 48$. Or, conversely, FI 48 should indicate a total of 65 individuals within the 100 quadrats. But since plants are not distributed entirely at random, the actual number is therefore always greater than indicated by the mathematical formula, which may be expressed, when $q = 100$, as $n = \frac{\log\ (1 - FI)}{\log\ 0.99}$. Thus, *Pteris aquilina*, determined by actual count to have an average abundance of 4,400 in 100 quadrats, has FI 99, corresponding to a theoretical number of only 455 individuals. Obviously, the

discrepancy between actual and theoretical number should be, and is, greatest in species of high frequency, *FI* 95 or more. It is not possible to draw any accurate conclusions as to the relation between theoretical and actual number of individuals, but in general, the theoretical number is one fifth to two thirds as large as the actual, and results any more accurate than this are probably of little or no value in ecological description.

The determination of the proper size of the major quadrat involves reducing the original series of quadrats to a smaller number of larger quadrats, thereby increasing the frequency index of selected species to 99 or more. With *FI* 99 or more for all the important species, it may be assumed that this quadrat is large enough to serve as a fair sample of the association.

In the original equation $1 - \left(1 - \frac{1}{q}\right)^n = FI$, substitute for q the number of quadrats actually counted, use for *FI* the index of the least common one of the important species, and solve for n. Substitute again the determined value for n and 99 for the original *FI* and solve for q. The equation is $1 - \frac{1}{q} = \sqrt[n]{.01}$ (presuming 100 quadrats were counted), from which q may be easily determined. For example, in a certain association, it is desired to determine a major quadrat which will probably contain all the species with *FI* 60 or more.

$$1 - \left(1 - \frac{1}{100}\right)^n = 60: \; n = 90$$

$$1 - \frac{1}{q} = \sqrt[90]{.01}: \; q = 20 \text{ (fractions omitted)}$$

That is, the original 100 quadrats redivided into 20 larger quadrats should show *FI* 99 or 100 for all species which originally had *FI* 60 or more; or the major quadrat should be five times as large as the original. The error concerned in computing the value of n, due to imperfect distribution of the species, does not affect this last equation, and experience has shown that it gives surprisingly good results. On the average, four major quadrats out of five, the location of which is chosen at random, present all the important species for which they were computed.

Jaccard's *community coefficient* (*CC*) was designed to express by a number the degree of similarity between two areas of vegetation. His method is to divide the total number of species in both areas into the number common to both. Thus, two areas, each containing 30 species, of which 20 were common to the two, contain a total of 40 species, and the community coefficient is accordingly 50. Jaccard's method fails to take account of the much greater importance of some abundant species, and the resulting error of computation may be obviated, in part at least, by weighting each species with its frequency index. Referring to columns 5 and 6 of TABLE I, and weighting each species with its average index in both columns, the results, shown in TABLE II

TABLE II

	In first area only	Common to both areas	In second area only
Pteris aquilina		99	
Vaccinium pennsylvanicum		80	
Gaylussacia baccata		42.5	
Aster laevis		33.5	
Carex umbellata		38.5	
Rhus glabra		24	
Rumex Acetosella		20	
Rubus allegheniensis		26	
Panicum boreale		8.5	
Danthonia spicata		25	
Gaultheria procumbens		13.5	
Gnaphalium decurrens		11	
Populus grandidentata			5
Hieracium venosum		5	
Erigeron canadensis	2.5		
Panicum xanthophysum			1
Diervilla Lonicera	7.5		
Solidago canadensis	1		
Agrostis hyemalis		4.5	
Lactuca canadensis	1.5		
Poa compressa		2.5	
Quercus rubra	1		
Comandra umbellata			1.5
Amelanchier canadensis			1
	13.5	433.5	8.5

are obtained, from which the community coefficient of the two areas concerned is determined as 95, by dividing the sum of the three columns, 455.5, into the sum of the center column.

By Jaccard's method, giving equal weight to each species, 24 total species divided into 15 common species = *CC* 62.

This method, while doubtless better than the original one, is still deficient in allowing equal weight to such small slender plants as *Erigeron canadensis* and large bushy ones as *Gaylussacia baccata*. If each plant could be further weighted by a multiplier expressive of its size, a better index would doubtless be attained. In this particular case, for example, each plant of the latter species occupies probably 400 times as much ground space as the former. So far no serious attempt has been made to follow out this suggestion.

It is freely admitted that the expression "*FI* 55" means little to a person who has not already experienced its meaning by actual field work. But to such persons it does present at once an idea of the relative abundance of that particular species, and an idea much more accurate than any such general expression as *common*, *rare*, or *copious*. Students who have used the method adopt it into their scientific vocabulary and actually use it in their conversation, almost as freely as they refer to degrees of temperature. The writer has heard a student, describing the luxuriant growth of *Epilobium angustifolium* following a recent fire, state that it must have had "a frequency index at least 90," instead of resorting to the usual hyperbolé to express great abundance, or, in alluding to a new station for a *Habenaria*, say "There was a good deal of it all through the woods: *FI* probably 5 or 10." And if such a student should read an account of an utterly unfamiliar vegetation in some remote part of the world, in which the frequency indices were given, he would at once have a relatively clear idea of the actual conditions.

Nevertheless, the quantitative study and description of vegetation are still in their infancy, and there is every opportunity for great improvement.

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1914–1919

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Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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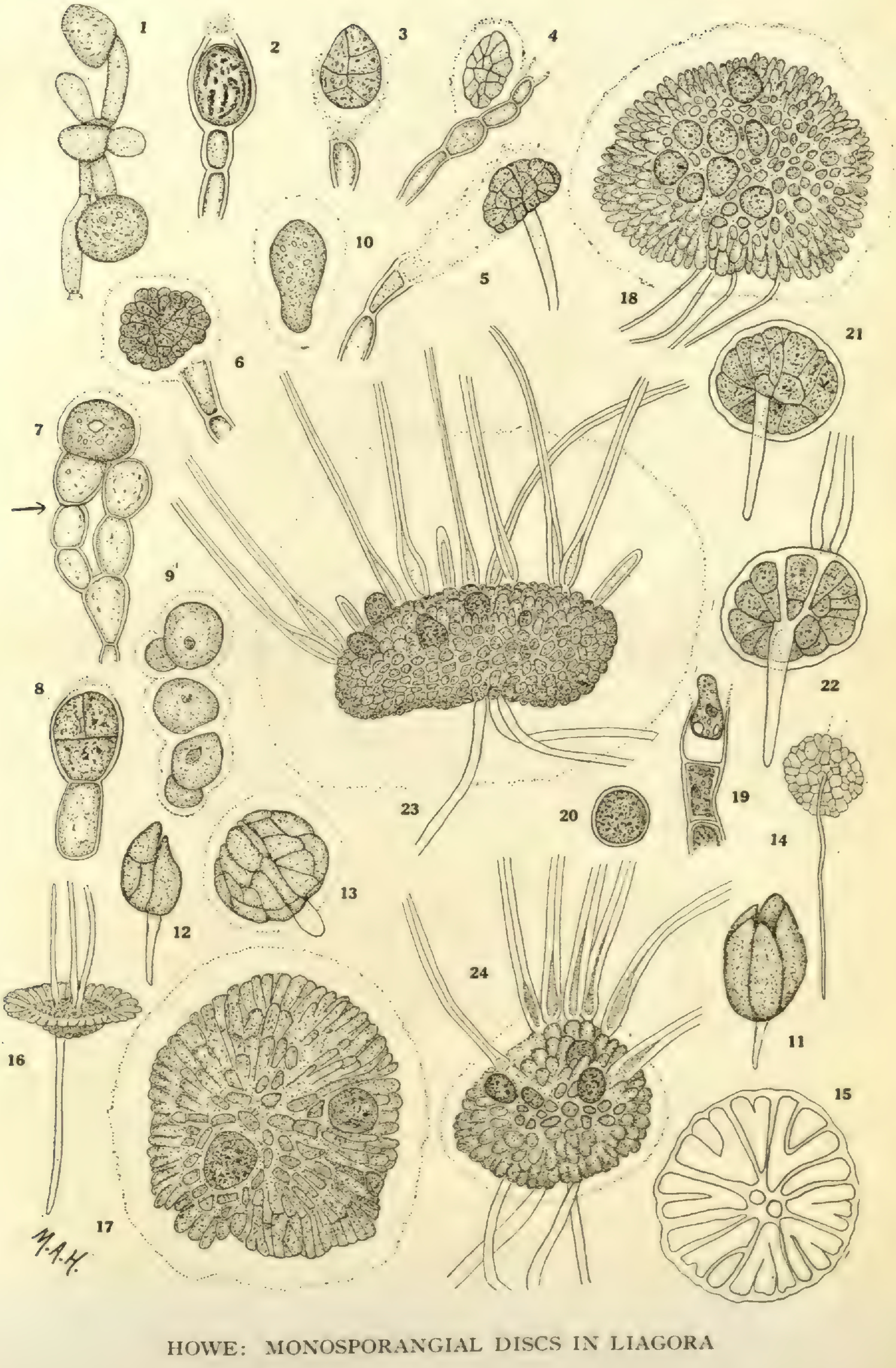

HOWE: MONOSPORANGIAL DISCS IN LIAGORA

Vol. 47 No. 2

BULLETIN

OF THE

TORREY BOTANICAL CLUB

FEBRUARY, 1920

Notes on Rosaceae—XII

PER AXEL RYDBERG

ROSES OF NORTHEASTERN NORTH AMERICA

By northeastern North America is meant the parts of the United States and Canada east of the Mississippi River and the Lake of the Woods and north of North Carolina and Tennessee. It comprises about the same region as that covered by Gray's and Britton's manuals, except the extreme western portion included in the latter.

As the genus *Rosa* is too large to be treated in one paper, my intention has been to discuss the different species according to their distribution, in six or seven articles. One of these articles, entitled "Roses of California and Nevada,"* has already been published; the roses of the Rocky Mountain Region have been described in my Flora,† and the whole genus, as represented in North America, has been monographed in the North American Flora.‡ There is, therefore, no need of giving full descriptions or of citing lists of synonyms. For the sake of those who do not have access to the later publication, it may be desirable to include keys to the species. The articles will otherwise contain only such notes as could not be included in the North American Flora.

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* Bull. Torrey Club 44: 65–84. 1917.

† Flora of the Rocky Mountains and adjacent plains. New York. 1917.

‡ N. Am. Flora 22: 483–533.

[The BULLETIN for January (47: 1–44, *pl. 1*) was issued February 18, 1920.]

Key to the groups

Styles much exserted, united, about equaling the stamens; stipules adnate; sepals reflexed, deciduous; stem climbing, with curved prickles. — I. SYNSTYLAE.

Styles not exserted, or only slightly so, distinct; stigmas forming a head closing the mouth of the hypanthium.

Stipules almost free from the petioles; introduced climbers or trailers. — II. BRACTEATAE.

Stipules for most of their length adnate to the petioles; plants rarely climbing.

Sepals after flowering reflexed and soon deciduous.

Achenes inserted both on the inner walls and in the bottom of the hypanthium; prickles rarely infrastipular.

Stem prickly.

Leaflets 3–5, rarely 7, large, round; stem with both scattered prickles and bristles; flowers mostly solitary. — III. GALLICAE.

Leaflets mostly 7; stem with strong prickles, very rarely with bristles. — IV. CANINAE.

Stem unarmed. — VI. CINNAMOMIAE.

Achenes inserted only in the bottom of the bristly hypanthium; stem with infrastipular prickles and usually with numerous bristles on the young shoots. — V. CAROLINAE.

Sepals after flowering erect, connivent, long-persistent on the fruit; achenes inserted both on the inner walls and in the bottom of the hypanthium.

Flowers corymbose or, if solitary, then supported by a bract; leaflets large.

Stem with scattered prickles, rarely with intermixed bristles; sepals more or less lobed; foliage glandular-punctate, sweet-scented (in *R. rubiginosa* and *R. tomentosa*). — IV. CANINAE.

Stem, at least the young shoots, bristly; prickles infrastipular or lacking; sepals entire or the outer sometimes with one or two lobes; foliage not very sweet-scented. — VI. CINNAMOMIAE.

Flowers solitary, bractless; leaflets very small. — VII. PIMPINELLIFOLIAE.

I. SYNSTYLAE

Stipules pectinate. — 1. *R. multiflora.*

Stipules entire or denticulate.

Leaflets glabrous or slightly pubescent on the veins beneath, dark green and shining above. — 2. *R. setigera.*

Leaflets velutinous-pubescent beneath, rather dull above. — 3. *R. rubifolia.*

1. ROSA MULTIFLORA Thunb.

This species is a native of Japan and China. It is extensively cultivated, and has developed into numerous horticultural varieties, mostly with double flowers. Numerous hybrids have also been produced. It has become naturalized in Alabama and on Porto Rico, and is otherwise found occasionally escaped in the Southern States. Within the area covered by this paper, there is a simple record from Maryland. The species is distinguished from its relatives by the fringed stipules.

2. ROSA SETIGERA Michx.

This is a native of the Southern States and is common from North Carolina and Kentucky to Alabama and Florida. It is found, however, outside of this range as far west as Kansas and Arkansas. The following localities north of Kentucky have been recorded. The specimens collected at these places might have been from plants escaped from cultivation.

NEW YORK: Oneida, *Maxon;* Ithaca, *Coville.*

3. ROSA RUBIFOLIA R. Br.

This species has been regarded as the same as the preceding. In its typical form, however, with its broader and thicker leaflets densely pubescent beneath, it seems quite distinct. The few intermediate forms seen by the author may have been hybrids. *R. rubifolia* has its best development in the Mississippi Valley and is rare east of the Alleghanies. It extends further north than *R. setigera.* The following specimens are here recorded from outside of the range proper. These may have been collected from escaped plants, as this species, as well as *R. setigera,* is extensively cultivated.

NEW JERSEY: Milburn, *Mackenzie.*

ONTARIO: Sandwich and Pelee Island, *Macoun.*

II. BRACTEATAE

One species. 4. *R. bracteata.*

4. ROSA BRACTEATA Wendl.

A native of China, often cultivated and occasionally escaped and naturalized from Virginia to Florida and Texas. It is well

understood and no specimens need to be cited. The only synonyms the author has found, are: *R. lucida* Lawrence, and *R. Macartnea* Dum. Cours. The former is a hyponym and a homonym. The latter has often been given as a synonym of *R. laevigata*, but erroneously so, for it is easily seen from Dumortier's description that it belongs to *R. bracteata*.

III. GALLICAE

One species. 5. *R. gallica*.

5. ROSA GALLICA L.

Cultivated in many forms and occasionally escaped. Some of these escaped specimens may belong to the pure-blooded *R. gallica*, but others are plainly referable to *R. centifolia*. Whether or not the latter is a distinct species is a question which I have had neither the time nor the inclination to settle. The following specimens, belonging to *R. gallica* or closely related species, have been recorded within the area.

NEW YORK: New Baltimore, *N. Taylor*.

WISCONSIN: *Stennett*.

IV. CANINAE

Leaflets glandular-pruinose beneath, distinctly double-serrate with gland-tipped teeth.

Leaflets suborbicular or broadly oval, mostly rounded at the apex; hypanthium in fruit obovoid or broadly ellipsoid, abruptly contracted at the apex; sepals tardily deciduous or more or less persistent; styles pubescent. 6. *R. rubiginosa*.

Leaflets ovate or oval, acute or short-acuminate; hypanthium in fruit narrowly elliptic, tapering at both ends; sepals rather early deciduous; styles glabrous or nearly so. 7. *R. micrantha*.

Leaflets not glandular beneath, except sometimes on the midrib; teeth only occasionally double.

Leaves pubescent, at least beneath, and on the rachis. 8. *R. dumetorum*.

Leaves glabrous on both sides, shining above. 9. *R. canina*.

6. ROSA RUBIGINOSA L.

The Sweetbrier is often cultivated and has become thoroughly naturalized in many places. It is very variable in cultivation and the naturalized specimens show also such variation. All specimens labeled *R. rubiginosa* do not, however, belong to that species. At least one-fourth of them belong to the next.

7. ROSA MICRANTHA Borrer

This is often mistaken for *R. rubiginosa* but differs in the less rounded leaflets, the more ellipsoid fruit, the more deciduous sepals, the smaller petals, and the almost glabrous styles. The following specimens belong to it:

MASSACHUSETTS: Manchester, *Chamberlain;* Ipswich, *Morong.*
NEW YORK: Oak Point, *Burnham 77;* High Bridge, *Elizabeth Knight;* Fort Lee, *Torrey Botanical Club.*
NEW JERSEY: Rocky Hill, *Lighthipe;* Great Notch, *Nash 1056.*
MARYLAND: Rush River, *Shull 347.*
VIRGINIA: Bedford, *A. H. Curtiss.*

8. ROSA DUMETORUM Thuill.

Closely resembling the Dog Rose but with the leaves pubescent beneath. The only record of this species from America is one from Bowling Green, Kentucky. This might have been an escape from cultivation.

9. ROSA CANINA L.

The Dog Rose is well understood, though it is only sparingly naturalized in the Northeastern States.

V. CAROLINAE

Hypanthium globose or short-ellipsoid, rounded or barely acute at the base.
Infrastipular prickles decidedly curved.
Leaflets finely serrulate, elliptic or oblanceolate; prickles short and stout.
Leaflets mostly 7; flowers usually corymbose on erect branches; fruit depressed-globose, about 12 mm. thick. 10. *R. palustris.*
Leaflets mostly 5; flowers usually solitary or two together on spreading branches; fruit ellipsoid, acute at the base, 8–9 mm. thick. 11. *R. dasistema.*
Leaflets coarsely serrate, oval or obovate.
Leaflets not shining; prickles short and weak.
Leaflets obovate; fruit 10–12 mm. in diameter. 12. *R. gemella.*
Leaflets oblanceolate; fruit 7–10 mm. in diameter. 13. *R. nanella.*
Leaflets shining; prickles long and stout. 14. *R. virginiana.*
Infrastipular prickles straight or slightly curved.
Leaflets oval or obovate or broadly lance-elliptic, 5–7 (in *R. virginiana* rarely 9).

Leaves decidedly pubescent beneath. 15. *R. Lyoni.*
Leaves glabrous or pubescent only on the veins beneath.
Leaflets shining above; flowers usually corymbose; prickles as a rule stout and flattened at the base. 14. *R. virginiana.*
Leaflets not shining above; flowers usually solitary, rarely a few together; prickles slender, terete.
Leaflets not glandular-dentate.
Plant low, usually less than 2 dm. high; leaflets less than 2 cm. long, dark green; prickles 3–5 mm. long, stout, often curved. 13. *R. nanella.*
Plant usually more than 2 dm. high; leaflets usually more than 2 cm. long; prickles more than 5 mm. long, slender.
Leaflets broadly oval. 16. *R. obovata.*
Leaflets elliptic or narrowly oval. 17. *R. carolina.*
Leaflets glandular-dentate and rachis usually glandular. 18. *R. serrulata.*
Leaflets narrowly elliptic or lance-oblong, usually 9–11, at least on the new shoots. 19. *R. nitida.*
Hypanthium decidedly pyriform, or ellipsoid, long-tapering at the base. 20. *R. Bicknellii.*

10. ROSA PALUSTRIS Marsh.

This has usually been known as *Rosa carolina* L. It is the *R. carolina* of the second edition of Linnaeus's Species Plantarum, but not that of the first. It is evident that Linnaeus, when he prepared the manuscript for the first edition, did not have any specimens, but based his *R. carolina* wholly on the plate and description in Dillenius's Hortus Elthalmensis, *pl. 245, f. 316.* This plate does not represent *R. carolina* as usually understood, but the species commonly known as *R. humilis* Marsh. In discussing *R. carolina*, Crépin states: "The latter description, i.e., that of Hortus Elthalmensis, and the figure can apply either to *R. humilis* Marsh. or to *R. lucida* Ehrh., but not to *R. carolina* as we know it today. Besides the branch which I have seen in Sherard's herbarium with Dillenius's name on, belongs to *R. humilis* Marsh (= *R. parviflora* Ehrh.). The result is that the first name for *R. humilis* Marsh. is *R. carolina* L. Sp., ed.1." Crépin therefore arrived at the same conclusion as I. The oldest

name for the Swamp Rose, or what has usually been known as *R. carolina*, is thus *R. palustris* Marsh., a very appropriate name. The synonymy of this species is much involved; see North American Flora.

West of Lake Michigan, especially in the Green Bay region, *R. palustris* has more pubescent, smaller, and less bluish green leaflets. This form may represent a distinct species or geographical variety.

11. ROSA DASISTEMA Raf.

Some specimens, collected especially in Missouri and named *R. carolina*, differ from *R. palustris* in having a smaller hypanthium decidedly pear-shaped and acute at the base, instead of depressed-globose and rounded below, and also in having fewer leaflets, usually five, rarely seven, instead of seven or nine. These specimens agree closely with the description of *R. dasistema* Raf. The type of the latter was from Indiana, from which state I have seen no specimens. This fact, however, does not disprove the identity of the Missouri specimens with Rafinesque's species. These specimens are:

MISSOURI: Paw Paw Junction, *Bush 226;* Kennett, *Trelease 177;* Campbell, *Bush 109, 6214;* Butte County, *Bush 3688.*

12. ROSA GEMELLA Willd.

Although this has usually been regarded as a synonym of *R. blanda*, the description shows that it can not be that species. The description of the prickles of *R. gemella* (slender and curved) would exclude it from *R. blanda.* There is, however, a plant, though rather rare, which answers Willdenow's description. It is related to *R. carolina*, but differs in the curved prickles, the more corymbose inflorescence, and the entire sepals. It may be confused also with *R. virginiana* and *R. palustris.* From the former it differs in the thin dull leaflets, the slender more curved prickles and the low habit. Its prickles resembles those of *R. palustris* but are much weaker, while its leaflets are broad and rather short and more coarsely serrate. The following specimens belong here:

NOVA SCOTIA: Yarmouth, *Howe & Lang 122.*

MASSACHUSETTS: Ipswich, *Nash, Morong;* Provincetown, *Hollick.*

NEW YORK: South Beach, Staten Island, *Burnham 746;* New Dorp, *Kearney;* Eastport, *Schrenk.*

VIRGINIA: Marion, *N. L. & E. G. Britton & A. M. Vail.*

13. ROSA NANELLA Rydberg

Mr. E. P. Bicknell collected a small rose on the sand-dunes of Chappaquiddick Island, east of Martha's Vineyard, Massachusetts, which was described in the North American Flora under this name. It is related to *R. carolina,* but smaller, has smaller leaflets, smaller fruit, and short, usually curved prickles. It also resembles *R. nitida,* especially in the small shining leaflets, but the latter are fewer in number and more obovate, and its prickles are different. The following specimens belong here:

MASSACHUSETTS: Chappaquiddick Island, *Bicknell.*

NEW YORK: Peconic River, Long Island, *N. Taylor;* Smith's Point, Fire Island, *E. L. Morris;* Oak Island, *N. Taylor.*

14. ROSA VIRGINIANA Mill.

This has usually been regarded as a synonym of *R. blanda.* This may have been due partly to the fact that Miller described *R. virginiana* as unarmed, partly perhaps to the fact that at least one of the specimens on which *R. blanda* was originally based belonged to the species here treated. Another character assigned to *R. virginiana* by Miller, viz., "the shining leaves," does not very well apply to *R. blanda* as usually understood. The name *R. virginiana* Mill. was substituted for *R. lucida* Ehrh. in the New Gray's Manual by Robinson and Fernald. I therefore wrote to Professor Fernald, asking him kindly to let me know the reasons for the change made. In answer I received the following letter, which I take the liberty of publishing:

Rosa virginiana Miller, Gard. Dict. ed. 8, no. 10 (1769), is represented by a fine sheet in the herbarium of the British Museum, marked "*Rosa virginiana* Mill. Dict. No. 10!" James Britten and J. G. Baker who called my attention to it say there is absolutely no question about its authentity. There are three fruiting branches and they are perfectly good *R. lucida* Ehrh. Crépin recognized it and has written on the sheet "*R. lucida* Ehrh. Cr." and J. G. Baker (Jour. Linn. Soc. XXXVII. 74) in his Revised Classification of Roses so treats it. I took a photograph—an excellent one nearly life-size—and it shows the characteristic broad-base and curved infra-stipular prickles at two points.

It is therefore plain that *R. virginiana* Mill. is the oldest name for the rose usually known as *R. lucida* Ehrh. To me it seems that *R. carolinensis* Marsh. applies better to this species than does either of the two species described by Linnaeus under the name of *R. carolina*. *R. rapa* Bosc is apparently a double form of this species.

Mr. Best reduced this species to a variety of *R. humilis*. He had collected a great number of rose-specimens in New Jersey. Some of these were presented to Columbia University. These show many gradations between *R. lucida* Ehrh. and *R. humilis* Marsh. (i.e., the original *R. carolina* L.), and also between these and another form, *R. humilis villosa* Best (*R. Lyoni* Pursh). Best concluded that all should be regarded as a single variable species. He has been followed by N. L. Britton and C. K. Schneider, the latter using the name *R. virginiana lucida* Best. I doubt if Best ever used said combination, at least in print. In my opinion several of Mr. Best's specimens are of hybrid origin, and this circumstance would give a satisfactory explanation for the intergradation, which is rarely met with elsewhere.

Rosa blanda Willmottiana Baker, according to the figure, has nothing to do with *R. blanda*, but belongs without doubt to *R. virginiana*.

15. ROSA LYONI Pursh

A species which has been confused with both *R. virginiana* Mill. (*R. lucida* Ehrh.) and *R. carolina* L. (*R. humilis* Marsh.), but which differs from both in having the leaves densely pubescent beneath. In general habit and in the sepals and the prickles, it resembles most the latter, but the leaflets are much broader and the flowers are as large as in *R. virginiana*. The flowers are also more inclined to be corymbose than in *R. carolina*. *R. Lyoni* is a more western species, receiving its best development in Missouri, but extends as far east as central New York and New Jersey, where it mixes with the two species mentioned, and hybridizes with them. See remarks under *R. virginiana*. *R. Lyoni* is apparently the same as *R. pusilla* Raf., *R. lucida* α T. & G., and *R. humilis villosa* Best.

16. ROSA OBOVATA Raf.

The first one to give a good description of this species was Lindley, who described it in his monograph under the name *R. laxa*. Unfortunately this name was preoccupied by *R. laxa* Retz., for which reason Sprengel substituted *R. Lindleyi*, also a homonym or rather pseudo-homonym, as there was already a *R. Lindleyana* Tratt. Mr. Baker, in Miss Willmott's Genus *Rosa*, described it as *R. humilis grandiflora*. There is, however, a *R. grandiflora* Salisb., so the name is not available. The only name left to consider is *R. obovata* Raf. Rafinesque's description, in this case as usually, is far from satisfactory, but "the single large flowers, obovate leaflets, and straight prickles," would indicate this species. In many respects it is intermediate between *R. virginiana* and *R. carolina*, but has comparatively broader leaflets than either. The leaflets are rather dull, sometimes somewhat glaucous. The following specimens are to be referred to it:

MAINE: Hudson, *Briggs;* Bangor, *O. W. Knight.*

MASSACHUSETTS: Nantucket Island, *Bicknell.*

RHODE ISLAND: Newport, *Mearns 553.*

NEW YORK: Ithaca, *Coville, Pearce;* Long Beach, Long Island, *Bicknell;* Lake Ronkonkoma, *Bicknell.*

NEW JERSEY: Bay Head, Ocean County, *Mackenzie.*

PENNSYLVANIA: Raymond's Kill, Pike County, *Nash.*

MISSOURI: Chadwick, *Trelease 185.*

17. ROSA CAROLINA L.

This name was taken up in the North American Flora for the plant described by Linnaeus in the first edition of his Species Plantarum. It is the same as *R. humilis* Marsh. and *R. parviflora* Ehrh. See the discussion under *R. palustris*. Wangenheim described it under the name *R. pennsylvanica*, and Michaux changed the form of the name to *R. caroliniana*. It appears also to be *R. pratensis* Raf. The rest of the synonyms are easily explained.

18. ROSA SERRULATA Raf.

This is closely related to the preceding species and has usually been confused with it. It differs in the double-toothed leaflets,

each tooth usually ending in a distinct gland. In the South it is more common than *R. carolina*, but extends as far north as central New York and Wisconsin. It is the same as *R. parviflora glandulosa* Crépin, and also as his var. *setigera*, at least in part.

19. ROSA NITIDA Willd.

This is well understood. It is distributed from Newfoundland to Massachusetts, near the coast, and has likewise been collected in Connecticut.

20. ROSA BICKNELLII Rydberg

This species is probably most closely related to *R. virginiana* but differs in the smaller and less numerous flowers, the obovoid fruit acute at the base, the smaller, thinner, and not shining leaflets. It may be the same as *R. acuminata* Raf., but the leaflets are by no means "acuminate," and the distribution, as far as known, is quite different. The following specimens belong to it:

NOVA SCOTIA: Purchell's Cove, Halifax Harbor, *Howe & Lang.*

MASSACHUSETTS: Coscati and Wauwinet, Nantucket Island, and Chappaquiddick Island, *Bicknell.*

NEW YORK: Long Beach, East Rockaway and Lawrence, Long Island, *Bicknell;* Lone Hill and Peconic River, *N. Taylor.*

VI. CINNAMOMIAE

Infrastipular prickles not present; branches unarmed or bristly, not prickly.
- Inflorescence corymbose, terminating the stem; plant more or less suffruticose; stem very bristly, mostly dying back to the ground in the winter; leaflets usually 9–11.
  - Leaves glabrous or nearly so. — 21. *R. arkansana.*
  - Leaves densely pubescent, especially beneath. — 22. *R. suffulta.*
- Inflorescence of solitary or few corymbose flowers ending lateral branches; plant shrubby; leaflets usually 5 or 7 (or 9 on the new shoots only).
  - Stem densely bristly even in age.
    - Leaflets comparatively thin, neither rugose nor strongly reticulate; branches and prickles glabrous.
      - Hypanthium decidedly pear-shaped or ellipsoid, acute at the base, with a distinct neck at the top. — 23. *R. acicularis.*

Hypanthium subglobose, without a neck.
Leaflets glandular-granuliferous and pubescent beneath; fruit 1.5 cm. thick. 24. *R. Bourgeauiana.*
Leaflets villous beneath; fruit about 1 cm. thick. 25. *R. acicularioides.*
Leaflets thick, strongly reticulate, and rugose; branches and even the prickles pubescent. 26. *R. rugosa.*
Stem unarmed or when young covered with more or less deciduous bristles.
Sepals erect or connivent in fruit.
Leaflets decidedly but finely pubescent beneath. 27. *R. blanda.*
Leaflets glabrous on both sides, shining. 28. *R. subblanda.*
Sepals reflexed in fruit.
Leaflets decidedly puberulent or short-pilose; sepals 9–15 mm. long; petals 1.7–2 cm. long. 29. *R. Williamsii.*
Leaflets glabrous or nearly so; sepals 2–5 cm. long; petals 2.5–3.5 cm. long. 30. *R. johannensis.*
Infrastipular prickles present, more or less curved.
Flowers mostly solitary; petals 2.5 cm. long or more: leaflets densely pubescent beneath. 31. *R. spinosissima.*
Flowers corymbose; petals about 2 cm. long; leaflets finely puberulent beneath. 32. *R. palustriformis.*

21. ROSA ARKANSANA Porter

Collected in Wisconsin.

22. ROSA SUFFULTA Greene

Collected near the Bureau of Standards, Washington, D. C. This and the preceding species belong to the prairies and plains west of the Mississippi River and will be treated in a subsequent article.

23. ROSA ACICULARIS Lindley

This species was originally described from Siberian material, but Alaskan specimens match exactly Lindley's figure and so do specimens from Siberia. Specimens from the southern and eastern limits of its range differ a little, in having smaller and less firm leaflets, less glaucous beneath, and smaller flowers. They differ from *R. Engelmannii* and *R. Bourgeauiana* in the leaflets, which are narrower and decidedly pubescent beneath; from the former in the simple teeth and the lack of glandular granules on the lower ieaf-surfaces, and usually in the larger fruit; and from the latter In the elongate fruit with a distinct neck. All specimens from

Wisconsin, Michigan, and northern New York, labelled *R. Engelmannii* and many labelled *R. Sayi* belong here. *R. Sayi* Schwein. is in reality a synonym of this. See discussion under the next species. Sometimes *R. acicularis* is nearly destitute of bristles, and may then be mistaken for *R. blanda*, but the ellipsoid fruit always distinguishes it. Such specimens are:

MICHIGAN: Presque Isle Park, Marquette, *Wheeler* (determined by Crépin as *R. blanda*, with the following remark, "fruiting receptacle resembling that of *R. acicularis* var. *Engelmannii*").

24. ROSA BOURGEAUIANA Crépin

This was first collected by Richardson on the Saskatchewan or somewhere between that river and the Mackenzie, and was published as *R. majalis* Borrer in Hooker's Flora. There is an older *R. majalis* Herm., however. In 1875, Crépin proposed the name *R. Bourgeauiana*, without a description, but the next year he reduced it to a variety of *R. acicularis*. Watson, in his Monograph of the North American Roses, adopted the name *R. Sayi* Schwein, and it has usually been known under that name. It is not *R. Sayi* Schwein., however, for Schweinitz described his species as having ellipsoid fruit and the leaves pubescent beneath. These characters point without any doubt to *R. acicularis*, which is also found in the region visited by Schweinitz. *R. Sayi* must therefore be regarded as a synonym of *R. acicularis*.

25. ROSA ACICULARIOIDES Schuette

Schuette's description* is very meager, but the writer has seen some of his specimens. The description in the North American Flora was drawn from those in the Gray Herbarium. Later some were also found at the New York Botanical Garden, among duplicates from Schuette's herbarium, received in exchange from the Field Columbian Museum, Chicago. The plant perhaps most resembles *R. Bourgeauinana* in habit, leaf-form, and size and form of the fruit, but the leaflets are densely pubescent beneath as in *R. acicularis;* yes, even more so, and with longer hairs. The specimens are from Lily Bay, Sturgeon Bay, and Little Sturgeon, Door County, Wisconsin.

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* Proc. Am. Ass. Adv. Sci. **46**: 278–9. 1898.

26. ROSA RUGOSA Thunberg

Common in cultivation and occasionally found as an escape; it is well established in a few places in Connecticut and on Nantucket Island.

27. ROSA BLANDA Ait.

The species was based on three different elements, judging from the following statements in the Hortus Kewensis:

> *Nat.* of Newfoundland and Hudson's-bay.
> *Cult.* 1773, by Mr. James Gordon.

Fernald* has properly discussed the status of the two native specimens covered by the description. Having previously discussed the matter with him, the author agreed that the name must be applied to the Hudson Bay specimen, rather than the Newfoundland one, for the plant is named the "Hudson Bay Rose,"* and the hypanthium is described as glabrous. Prior to this discussion with Professor Fernald, I had held the opinion that the Newfoundland plant should be regarded as the type, partly because Solander, who prepared part of the manuscript for the first edition of Aiton's Hortus Kewensis, had in manuscript called this *R. blanda* and the Hudson Bay shrub *R. blanda* β; and partly because *R. blanda* is described as glabrous. I therefore adopted the name *R. Solanderi* Tratt. for the shrub usually called *R. blanda*, the species with pubescent leaves. Having conceded to Fernald's argument, I have left *R. blanda* as interpreted by Lindley. If the name *R. blanda* is applied to the Newfoundland plant, it would become a synonym of *R. virginiana* and be eliminated altogether.

In the Green Bay region of Wisconsin and Upper Michigan, *Rosa blanda* is much more pubescent than elsewhere, so far as I know, and the pubescence of the lower surface of the leaves is sometimes as as long as in *R. acicularis* and *R. acicularioides*. In some of these specimens the leaflets are more elongate-elliptic and the hypanthium more elongate, or pear-shaped, or with a distinct neck, and in such cases the specimens are probably of hybrid origin, i.e., represent *R. acicularis* × *blanda*. In the same region *R. palustris* is also more pubescent. Could, perhaps, some *R. acicularis* blood have been infused in both many generations back?

* Rhodora **20**: 90–96. 1918.

Lindley recognized a so-called glabrous *R. blanda* and described it under the name *R. fraxinifolia* Borkh., but Borkhausen's description does not agree with Lindley's conception of *R. fraxinifolia*. Neither does C. C. Gmelin's description,* which has been cited as a synonym of *R. blanda*. Lindley included in this *R. fraxinifolia* not only *R. blanda* α of Solander's manuscript, i.e., the Newfoundland rose, but also the *R. blanda* described and figured by N. J. Jacquin† The former is, as shown by Fernald, nothing but *R. virginiana* Mill. and belongs to a different group, the CAROLINAE, instead of the CINNAMOMIAE. Jacquin's *R. blanda* is probably the same as the cultivated specimens mentioned by Aiton. Jacquin described *R. blanda* as being perfectly glabrous both as to the leaves and the hypanthium. His illustration does not in any way indicate that his plant was *R. virginiana*. In nearly every respect, it suggests *R. blanda*, except that both the illustration and the text inform us that it was glabrous. Is there such a plant, and what name should it bear? As stated before, Lindley recognized such a plant, though he erroneously included in it *R. blanda* α of Solander, from Newfoundland, which had a glandular bristly hypanthium. Neither can the name which he adopted be used for the reason given above. Crépin, who had seen the original specimens of *R. blanda* α, and had written on the sheet "verus *R. lucida*," i.e., *R. virginiana*, recognized a glabrous *R. blanda*, and described it as *R. blanda glabra*. As this plant evidently has no valid name, I gave it the name *R. subblanda* in the North American Flora.

28. ROSA SUBBLANDA Rydberg

This species is much rarer than *R. blanda* and wholly confined to the Northeast. The following specimens may be cited:

QUEBEC: *Mrs. Persival;* Cape Enrage, Bic, *Williams, Collins & Fernald.*

VERMONT: Gardener's Island, Lake Champlain, *Faxon;* Royalton, *Eggleston.*

NEW YORK: Bluff Point, Lake Champlain, *Vail.*

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* Fl. Bad. 2: 413. 1806.

† Fragmenta *pl. 107*. 1809.

29. ROSA WILLIAMSII Fernald

30. ROSA JOHANNENSIS Fernald

This and the preceding species have been discussed by their author,* and nothing more needs to be added.

31. ROSA SPINOSISSIMA L.

This is the earliest name for the Cinnamon Rose. Linnaeus probably included in the original description two different species, or at least cited also synonyms belonging to *R. pimpinellifolia*. Many authors have applied the name *R. spinosissima* to the latter species. It is evident that Linnaeus principally had in mind a native rose of Sweden, which could be none but the Cinnamon Rose.

Crépin† has shown that the original *Rosa cinnamomea* L., of the first edition of the Species Plantarum, which was based wholly on a plant from Switzerland and described by Haller and Bauhin, is the same as *R. pendulina* L. In the first edition Linnaeus gives as a synonym under *R. cinnamomea*, "Rosa sylvestris, odoratissimo rubro flore. *Bauh. pin.* 483." Under the same name, in the second edition, he cited, "Rosa, odore cinnamomi, simplex. *Bauh. pin.* 483," which shows that *R. cinnamomea* L. of the first edition was not the same as that of the second. The first was evidently what in the tenth edition of his Systema and in the second edition of his Species Plantarum is called *R. alpina*, which is the same as *R. pendulina* L.

The *R. cinnamomea* of the second edition is the plant usually known under that name. As stated before, the oldest name of this is evidently *R. spinosissima* L. Not that that name should be entirely equivalent to *R. cinnamomea* of the second edition, for Linnaeus evidently had two species confused. He gave two references under it, one to his Flora Suecica and the other to Bauhin's Pinax. The latter may well be *R. spinosissima* as usually understood, i.e., a form of *R. pimpinellifolia;* but the former must be something else. *R. pimpinellifolia* is not found, even as an escape, in the part of Sweden where Linnaeus reported his *R. spinosissima*. In his Flora Suecica, he gave the vernacular name

* Rhodora **20**: 94, 95. 1918.

† Bull. Herb. Boiss. **5**: 135–138. 1897.

of the plant in the province of Upland, north of Stockholm, and stated that it grew along margins of fields. Wahlenberg, both in his Flora Upsaliensis and in his Flora Suecica, identified it with *R. majalis* Retz. and *R. cinnamomea* Sm., which is the same as *R. cinnamomea* of the second edition of the Species Plantarum; he even adopted the name *R. spinosissima.*

In the tenth edition of his Systema, Linnaeus placed *R. spinosissima* in the second division, i.e., with the species having ovate fruit, while he placed *R. pimpinellifolia* in the first division with suglobose fruit. In the second edition of the Species Plantarum, he added nothing to what he had in the first edition except one sentence from the Systema. In his second Mantissa, he seems to have changed his views altogether. Under *R. pimpinellifolia* he made the following remark: "Cum *R. spinosissima* eadem facit *Hallerus.*" Evidently on account of Haller's interpretation, he adopted the name *R. spinosissima* for *R. pimpinellifolia.* He omitted all his previous synonyms, cited "*Clus. hist.* 1. *p.* 116," and made a new description, incorporating in it not only a globose fruit, but white petals, yellow at the base, characters all belonging to *R. pimpinellifolia.*

Rosa spinosissima (*R. cinnamomea* of the second edition of the Species Platarum) is in cultivation, and has been found occasionally escaped in the northeastern part of this continent, and also in Wisconsin.

32. ROSA PALUSTRIFORMIS Rydberg

This species was discovered by Dr. Schuette of Green Bay, Wisconsin, who distributed it under an untenable manuscript name. In habit, pubescence and prickles, it strongly resembles *R. palustris*, but the hypanthium and sepals are in form and size like those of *R. blanda.* The sepals are erect and persistent in fruit, while the hypanthium is glabrous, not glandular-hispid. At first I thought that it might be a hybrid between the two species, but it has one feature not found in either—the sepals are wholly without glands on the back, only with a few gland-teeth on the margins. In both *R. palustris* and *R. blanda*, the sepals are glandular on the back. The description in the North American Flora was drawn from the specimens in the Gray Herbarium. Those

received later, which are in the herbarium of the New York Botanical Garden, do not resemble *R. palustris* so much, but the distinctive characters are there. Besides the Green Bay specimens, there is also one from Neenah, Wisconsin.

VII. PIMPINELLIFOLIAE

One species.

33. *R. pimpinellifolia.*

33. ROSA PIMPINELLIFOLIA L.

As stated before, Linnaeus included this species under *R. spinosissima* in the first edition of the Species plantarum, but it is not the type of it. See the remarks under *R. spinosissima.* Many recent authors have readopted the name *R. pimpinellifolia* for the present species. I am glad that the latter name, which has been in use for this species during a hundred and fifty years, is to be taken up again.

R. pimpinellifolia is extensively cultivated and has escaped in many places. It has been mistaken for a native more than once. Pursh described it as *R. lutescens*, and lately E. G. Baker has given it another name, *R. illinoensis*. The latter was based on specimens collected, according to Baker, by Green, Lansing and Dixon at La Salle, Illinois. There is a sheet in the herbarium of the New York Botanical Garden, collected by Greenman [not Green], Lansing and Dixon. Baker distinguished it from *R. spinosissima* (i.e., from *R. pimpinellifolia*) by the smaller number of leaflets, only seven and by the upper prickles being paired under the leaves. In our specimens, some leaves have nine leaflets, while some of the upper leaves have only three or five. We have also some specimens from England and Scandinavia, which do not have more than seven leaflets. The arrangement of paired infrastipular prickles, I think, was only incidental, for our specimens, duplicates of the type, do not show this characteristic. *R. illinoensis* is nothing but the escape of one of the numerous cultivated forms of *P. pimpinellifolia*. The following American species belong to this species:

VERMONT: Johnson, *Grout.*

ONTARIO: Amherstbough, *Macoun 34752.*

ILLINOIS: La Salle County, *Greenman, Lansing & Dixon 133.*

HYBRIDS

It is well known that hybrids among roses are very common in cultivation, and many wild hybrids have been recorded in Europe. No attempt has been made in this country until recently to distinguish hybrids among our native species. The first and only record in print that I know of, was made in 1900 and by a European, Crépin, who published *R. carolina* × *nitida* in Rhodora. This hybrid should now be known as *R. nitida* × *palustris*.

Outside of this record, I did not know of anyone besides myself and Mr. E. P. Bicknell, who had undertaken to distinguish hybrids among our native roses, and neither of us had put our observations in print. Bicknell, who did so much in clearing up the *Rubus* hybrids, did some work on *Rosa* at the same time, though his notes have remained in manuscript.

While spending some time last fall at the Gray Herbarium, I found there a collection made by Dr. Schuette of Green Bay, Wisconsin, which collection I worked over in the light of a small paper published by him in 1889.* After my return to New York, I found that the New York Botanical Garden had received a set of Dr. Schuette's duplicates in exchange with the Field Columbian Museum in Chicago. The numerous notes accompanying these duplicates, as well as those at the Gray Herbarium, show that Schuette had done considerably more intelligent work than his published paper indicated. In his article, he described one new species, *R. acicularioides*, and several varieties of *R. blanda* and *R. carolina* (i.e., *R. palustris*). His descriptions are meager, mostly one or two lines long, and apparently of little value, unless studied in connection with his specimens. His notes, however, show that most of his varieties he regarded as hybrids between those two species and other roses found in the region. The notes if published would make a long paper by themselves. It would not be advisable to do so now, as nobody could now present the matter with Schuette's final views. It is evident that even at the time when he published his paper, he was inclined to regard these forms as hybrids. It is unfortunate that he did not dare or did not think it advisable to put his convictions in print and

* Proc. Am. Ass. Adv. Sci. 46: 278–279. 1898.

publish them as hybrids instead of varieties. His published paper does not give justice to his knowledge of, and insight into, the relationship of the roses of Green Bay and vicinity.

It is hardly worth while to redescribe our rose hybrids in this paper. Anyone who wishes to avail himself of descriptions can find them in the North American Flora. I shall therefore only indicate which hybrids have been recorded and cite some specimens which I regard as belonging to each.

ROSA ACICULARIS × BLANDA

WISCONSIN: Sturgeon Bay, Fort Howard, Elkhart, Little Sturgeon, and Lily Bay, *Schuette.*

MICHIGAN: Menominee, *Schuette.*

ROSA ACICULARIS × CAROLINA

WISCONSIN: Little Sturgeon, *Schuette.*

ROSA ACICULARIOIDES × CAROLINA

WISCONSIN: Lily Bay, Door County, *Schuette.*

ROSA BICKNELLII × NANELLA

MASSACHUSETTS: Chappaquiddick Island, *Bicknell.*

ROSA BICKNELLII × VIRGINIANA

MASSACHUSETTS: Squam, Nantucket Island, *Bicknell.*
NEW JERSEY: Farmingdale, *N. Taylor.*

ROSA BLANDA × CAROLINA

WISCONSIN: Peak's Point, Green Bay, Marinette, Dutch Creek, Peshtigo, Preble, and Big Swamico, *Schuette.*

ROSA BLANDA × PALUSTRIS

WISCONSIN: Fort Howard, Marinette, Green Bay, Big Swamico, *Schuette.*

ROSA BLANDA × VIRGINIANA

ONTARIO: Point Abino, *Small;* Mt. Denis, *Biltmore Herbarium.*
MICHIGAN: Ann Arbor (collector unknown).

ROSA CAROLINA × PALUSTRIS

NEW YORK: Jamaica, *P. Wilson;* Sylvan Beach, Oneida County, *House.*

PENNSYLVANIA: Island Park, near Easton, and on the Delaware, *Porter*.

NEW JERSEY: Spotswood, *N. Taylor*.

WISCONSIN: Big Swamico and Preble, *Schuette*.

ROSA CAROLINA × VIRGINIANA

NEW JERSEY: Farmingdale, *N. Taylor*.

INDIANA: Boss Lake, *Deam*.

ROSA DASISTEMA × VIRGINIANA

MISSOURI: Butler County, *Eggert*.

ROSA JOHANNENSIS × PALUSTRIS

MAINE: Portage Lake, *Robinson & Fernald*.

ROSA LYONI × SERRULATA

VIRGINIA: Marion and Rye Valley, *Small*.

WEST VIRGINIA: Little Falls, *Millspaugh;* White Sulphur Springs, *Biltmore Herbarium*.

NORTH CAROLINA: Matthews, *Biltmore Herbarium*.

GEORGIA: Floyd County, *Chapman;* Coosa River, *Biltmore Herbarium*.

ROSA LYONI × VIRGINIANA

NEW JERSEY: Kingswood and Rosemont, *Best*.

ROSA NITIDA × PALUSTRIS

MAINE: Foxcroft, *Fernald*.

ROSA NITIDA × VIRGINIANA

NEWFOUNDLAND: St. George, *Howe & Lang*.

MASSACHUSETTS: Branch Island.

ROSA PALUSTRIS × SERRULATA

WISCONSIN: Fort Howard, *Schuette*.

ROSA PALUSTRIS × VIRGINIANA

MASSACHUSETTS: Nantucket Island, *Bicknell*.

NEW JERSEY: Palisades: *Southwick*.

ROSA SERRULATA × VIRGINIANA

ALABAMA: Monte Sano and Auburn, *C. F. Baker.*

The following table indicates the hitherto recorded hybrids among our northeastern native roses:

	Rosa palustris	*Rosa dasistema*	*Rosa nanella*	*Rosa virginiana*	*Rosa Lyoni*	*Rosa carolina*	*Rosa serrulata*	*Rosa Bicknellii*	*Rosa nitida*	*Rosa acicularis*	*Rosa acicularioides*	*Rosa blanda*	*Rosa johannensis*
Rosa palustris				×		×	×		×			×	×
" *dasistema*				×									
" *nanella*								×					
" *virginiana*	×	×			×	×	×	×	×			×	
" *Lyoni*				×			×						
" *carolina*	×			×						×	×	×	
" *serrulata*	×			×	×								
" *Bicknellii*			×	×									
" *nitida*	×			×									
" *acicularis*						×						×	
" *acicularioides*						×							
" *blanda*	×			×		×				×			
" *johannensis*	×												

NEW YORK BOTANICAL GARDEN

Rare species of North American Diatomaceae

CHARLES S. BOYER

(WITH PLATE 2)

Auliscus floridanus sp. nov.

Valves subtriangular. Central space not evident. Surface of the valve plane, indistinctly pruinose for two thirds of the radius and abruptly costate near the border, with sharply defined, coarse costae at irregular intervals, parallel between the processes but converging near them. Processes three, close to the border, irregular or triangular, with hyaline margins. Diameter 70 μ. [FIG. 3.]

TYPE LOCALITY: Mosquito Inlet, Florida.

DISTRIBUTION: marine; known from the type locality only.

Auliscus hyalinus sp. nov.

Valve subcircular, plane, slightly irregular. Central space appearing hyaline, about one third the diameter of the valve, indistinctly granular or pruinose toward the border where finely punctate, subtle, radiating striae are interspersed at irregular intervals with delicate, costate lines. Processes three, with hyaline borders, placed at irregular intervals at a distance from the border greater than their diameter, indistinctly granular. Diameter 86 μ. [FIG. 4.]

TYPE LOCALITY: Savin Rock, Connecticut.

DISTRIBUTION: marine; known from the type locality only.

The granulation of the surface is somewhat similar to that of *A. pulvinatus* Grun. or *A. Le Tourneurii* Brun, except at the border.

Dimerogramma intermedium sp. nov.

Valves rhombic-lanceolate. Pseudoraphe indistinct. Striae ten in 10 μ, moniliform. Apices indistinctly punctate. Length of valve 35 μ. [FIG. 11.]

TYPE LOCALITY: Campeche Bay, Mexico.

DISTRIBUTION: marine; known from the type locality only.

Apparently intermediate between *D. fulvum* (Greg.) Ralfs and *D. minus* (Greg.) Ralfs.

Glyphodesmis tumida sp. nov.

Valves linear, tumid in the middle, with subcuneate ends. Central and terminal nodules distinct. Pseudoraphe distinct, widened in the middle. Striæ slightly radiating at the ends, moniliform, nine in 10 μ. Length of valve 95 μ. [FIG. 2.]

TYPE LOCALITY: Campeche Bay, Mexico.

DISTRIBUTION: marine; known from the type locailty only.

Resembles *Dimerogramma marinum* (Greg.) Ralfs in outline but differs in possessing a central nodule and finer striation. It differs from *Glyphodesmis Williamsonii* (Greg.) Grun. in outline and somewhat resembles *Plagiogramma Loczyi* Pant., considered by Brun a form of *G. Williamsonii*.

Glyphodesmis campechiana sp. nov.

Valves linear-lanceolate, tumid in the middle and tapering to the subacute ends. Central pseudonodule distinct; terminal spaces ovate. Striae marginal, twelve in 10 μ, leaving a broad, lanceolate, hyaline area about half the width of the valve. Length of valve 30 μ. [FIG. 10.]

TYPE LOCALITY: Campeche Bay, Mexico.

DISTRIBUTION: marine; known from the type locality only.

Synedra anguinea sp. nov.

Frustule in zone view sigmoid at the ends. Valves linear, sigmoid at the slightly tapering, rounded ends, pseudoraphe very narrow, somewhat indefinite. Striae nine or ten in 10 μ, radiate at the ends, punctate, interrupted by a marginal line on each side. Length of valve 315 μ. [Fig. 1.]

TYPE LOCALITY: Colon, Panama.

DISTRIBUTION: marine; known from the type locality only. Rare.

Synedra incisa sp. nov.

Valves linear-lanceolate, with subcapitate ends. One or both sides more or less deeply incised. Pseudoraphe scarcely evident. Striae about eighteen in 10 μ. Length of valve 25–50 μ. [FIG. 8.]

TYPE LOCALITY: Central City, Nebraska (in a water tank).

DISTRIBUTION: fresh water; known from the type locality only, where it is abundant.

Closely resembles *Synedra affinis Baileyana* H. H. Chase (in Walker & Chase, Some New and Rare Diatoms 4. *pl. 2, f. 1*)

in outline, but the striae are not marginal. The species was sent to me by Professor C. J. Elmore, Westminster College, Missouri.

Eunotia Stevensonii sp. nov.

Valves with arcuate dorsal margin and straight or slightly concave ventral margin tumid in the middle. Apices broad and rounded. Striae ten or eleven in 10 μ, punctate. A sutural line or pseudoraphe extends between the terminal nodules as in *E. americana* Kain & Schultze, *E. Clevei* Grun. and others. Length of valve 88–113 μ. [FIGS. 12, 13.]

TYPE LOCALITY: pond near Lake Sunapee, New Hampshire.

DISTRIBUTION: fresh water (fossil), in the Monmouth, Maine, peat deposit.

I take pleasure in naming this species after Mr. William C. Stevenson, Jr., mycologist, of Philadelphia, to whom I am indebted for numerous specimens.

NAVICULA ATTWOODII M. Perag. in Tempère, Diatomées du monde entier 100. 1915.

Valves linear-elliptical, with broad, rounded ends. Median line linear, narrow. Median pores somewhat incrassate. Terminal fissures indistinct. Striae finely lineate, ten to twelve in 10 μ, radiate in the middle, slightly convergent at the ends, interrupted in the middle by a broad expanding fascia reaching the margin. Length of valve 40–50 μ. [FIG. 9.]

TYPE LOCALITY: Quinnipiac, Connecticut.

DISTRIBUTION: marine; Baldwin's Creek, Long Island, and vicinity.

I had considered this form as new but Mr. Robert Hagelstein, who has collected numerous specimens, identifies it as Peragallo's species which, I believe, has not been figured.

Pinnularia Hagelsteinii sp. nov.

Valves rhombic-lanceolate, with produced, rounded ends. Striae marginal, absent from the middle of the valve, radiate in the middle, convergent at the ends, about twelve in 10 μ. Length of valve 60 μ. [FIG. 7.]

TYPE LOCALITY: near Bliss, Idaho.

DISTRIBUTION: fresh water (fossil), known from the type locality only; rather rare.

This form, of which several specimens have been found, occurs in material sent me by Mr. Robert Hagelstein, of Mineola, Long Island, after whom I take pleasure in naming it.

Nitzschia semicostata sp. nov.

Valves constricted in the middle, cuneate and acute at the ends. Longitudinal fold well defined. Keel puncta seven in 10 μ, extended into coarse costae to half the width of the valve, to 10 μ in length. Striae fourteen in 10 μ, punctate. Length of valve 115 μ. [FIG. 6.]

TYPE LOCALITY: Campeche Bay, Mexico.

DISTRIBUTION: marine; known from the type locality only; rare.

Near *N. subcostata* Grun., from which it differs chiefly in the length of the costae.

Surirella Palmeri sp. nov.

Frustule subcuneate, rounded at the ends. Valves ovate-oblong. Median line well defined. Costae three in 10 μ, reaching the median line, indistinct. Near the broad end of the valve a thin, triangular, fin-like blade, about 10 μ in length, ending in a sharp point, extends somewhat obliquely from the median line. Length of valve 108 μ. [FIGS. 14, 15.]

TYPE LOCALITY: Wawaset, Pennsylvania.

DISTRIBUTION: fresh water, known from the type locality only, where it is not rare.

I take pleasure in naming this form after Mr. T. Chalkley Palmer, of Media, Pennsylvania, who discovered it.

Kitton* has described and figured *Surirella Capronii* as resembling *S. splendida* (Ehrenb.) Kütz. in outline and costae but differing in possessing at one or both ends a "nipple-like process," hollow at the base, "with a short spine on the apex." In the present species the valve resembles *S. tenera* Greg. in outline and costae, while the process is quite different from that of *S. Capronii* Kitton.

In certain species of *Surirella* valves occur with a plasma pore, not, however, on the median line. The pore appears to serve as a medium of attachment to surrounding objects and would prevent the usual slow movement of the frustule. Whether the function

* Science Gossip 5: 61. 1869.

of the fin-like blade, acting as an anchor, serves a similar purpose, is a question.

ABNORMAL FORM OF AULACODISCUS OREGONUS Harv. & Bail.

In an article entitled, "*Aulacodiscus oregonus* with two centres," Dr. Christopher Johnston* describes and illustrates a form which he considers "as an evidence of the action of an excessive developmental potency." In normal forms of *A. oregonus* the processes, although variable in number, are symmetrically arranged near the border. In a specimen discovered by Mr. William C. Stevenson, Jr., of Philadelphia, in recent material from Monterey Bay, California, the valve is divided, somewhat asymmetrically, into six parts, each of which contains a hyaline centre and processes with more or less evident furrows. The form may be abnormal but Mr. H. C. Wheeler, of Montreal, has sent me two specimens mounted from material from Port Townsend, Washington, one of which somewhat resembles Mr. Stevenson's form, which is illustrated in FIG. 5, while the other is symmetrically divided into two parts separated by a hyaline space, with processes disposed regularly on each side exactly as in Johnston's form. Whether these specimens are evidences of the formation of gonidia may be a question, but they appear to be too numerous to be considered as mere abnormalities. It is to be noted that numerous valves occur in rich gatherings much smaller than the normal valve and of uniform size, equal to that of the partially formed valves in the specimen figured. In each of the specimens examined the internal finely granular plate described by Mr. R. C. Greenleaf† is distinctly shown, but its function in the formation of new valves is problematical.

* Am. Jour. Micros. 1: 82. 1876.

† Mo. Micros. Jour. 2: 326. 1869.

Explanation of plate 2

The figures are all magnified 600 diameters.

FIG. 1. *Synedra anguinea* Boyer.
FIG. 2. *Glyphodesmis tumida* Boyer.
FIG. 3. *Auliscus floridanus* Boyer.
FIG. 4. *Auliscus hyalinus* Boyer.
FIG. 5. *Aulacodiscus oregonus* Harv. & Bail., abnormal form.
FIG. 6. *Nitzschia semicostata* Boyer.
FIG. 7. *Pinnularia Hagelsteinii* Boyer.
FIG. 8. *Synedra incisa* Boyer.
FIG. 9. *Navicula Attwoodii* M. Perag.
FIG. 10. *Glyphodesmis campechiana* Boyer.
FIG. 11. *Dimerogramma intermedium* Boyer.
FIGS. 12, 13. *Eunotia Stevensonii* Boyer.
FIGS. 14, 15. *Surirella Palmeri* Boyer.

The wood of Machaerium Whitfordii*

ROBERT B. MILLER

(WITH EIGHT TEXT FIGURES)

MATERIAL

The specimen of wood described in this paper is from the type tree of a recently described species of *Machaerium*, known as *Machaerium Whitfordii* Macbride, and is No. 415 in the collections of the Yale School of Forestry. It was collected in the forest along the Negro River in Colombia, in July, 1917, by Dr. H. N. Whitford. The tree, according to the collector, is fairly common in the high hills of Colombia, attains a height of about 20 meters and is of commercial importance. The natives call it "negrillo," a name suggested by the dark color of the heartwood and not restricted to this species. It "belongs to the section *Oblonga* and is most closely related to *M. Moritzianum* Benth. and *M. sordidum* Benth."† It is related also to the true rosewoods of commerce.

The purpose of this paper is to supplement the botanical description of Macbride with a study of the wood structure. The wood presents some interesting features of value for diagnostic purposes. Unfortunately there is no authentic material of other species of *Machaerium* wood available with which to compare the new species.

GROSS AND LENS CHARACTERS

The wood of *Machaerium Whitfordii* is very hard and compact, without pronounced taste or odor, fine and uniform in texture, more or less cross-grained but apparently of good cabinet qualities. The sapwood, which in this specimen is 13–25 mm. thick, is cream-colored, while the heartwood, which suggests black walnut in color, varies from chocolate-brown to black, and is streaked. The line

* Contribution from the Yale School of Forestry, No. 9.

† Macbride, J. F. Contr. Gray Herb. II. 56: 53. 1918.

of demarcation between heartwood and sapwood is irregular both in general outline and detail and is independent of the concentric rings of growth.

The following figures show the comparative density of heartwood and sapwood after being dried to a constant weight at a temperature of 100° C. The greater density of the heartwood is

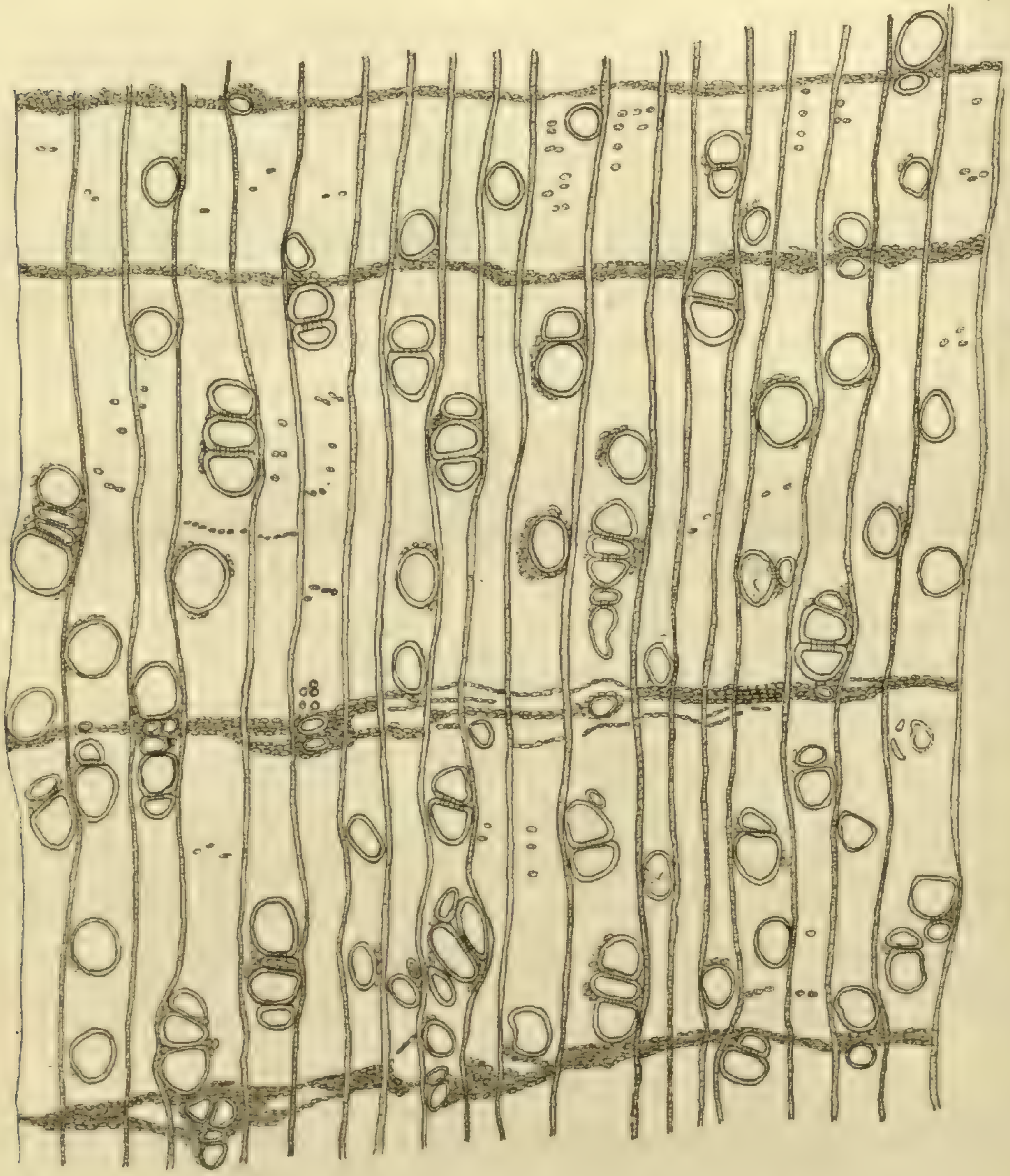

FIG. 1. Plan of cross-section showing four lines of terminal parenchyma limiting growth rings; also paratracheal and diffuse parenchyma.

due to infiltrations and, especially, to gum deposits in the vessels and parenchyma cells.

(1) All heartwood	1.118
(2) Five-sixths heartwood	1.108
(3) All sapwood	.975

Growth rings (FIG. 1), which presumably do not correspond to annual periods, are visible and are demarcated by terminal wood parenchyma which forms a single or sometimes double or triple line. These rings exhibit considerable variation in width. The pores are numerous, solitary or in small groups (usually radial), diffused irregularly throughout the ring or, occasionally, in echelon arrangement. They are of fairly uniform size throughout and are barely visible to the unaided eye.

The rays are not visible on the cross section without a lens. They are numerous, fine and uniform. On the tangential section they are seen (under the lens) to be of equal height and arranged in horizontal seriation, thus giving rise to fine and uniform transverse lines, the so-called "ripple marks," which, in proper light, may be seen with the unaided eye.

The bark of the specimen studied is 1.5–2 mm. in thickness and is composed of numerous fine uniform concentric laminations. The outer surface is of a grayish brown color, finely granular, smoothish, with occasional small flakes. The inner surface is somewhat ribbed vertically to correspond with the small irregularities on the outer face of the wood, and exhibits "ripple marks" very distinctly under the lens.

MINUTE ANATOMY

Vessels.—The vessels in cross section (pores) are circular, elliptical or oval in shape; some of them, as a result of crowding in groups, appear to be subdivided radially (FIG. 2). When elliptical, the tangential diameter is 0.075–0.09 mm. and the radial 0.10–0.12 mm. The thickness of the walls varies from 3 μ to 15 μ,

The vessels are without tyloses. Gummy contents, which are light-colored and not very pronounced in the sapwood, are dark brown and conspicuous in the heartwood, often completely filling entire segments. This material is sparingly soluble in hot water and insoluble in alcohol, though shrinking slightly upon dehydration. It appears unaffected by hydrofluoric acid.

The vessel segments are mostly straight, with slight constrictions at each end, the perforations are simple, the annular ridge is narrow, and the plane of contact is horizontal or slightly oblique. The segments are of nearly uniform length, mostly 0.20–0.21 mm., and are arranged in horizontal seriation.

The only markings on the walls are the pits. Those between two vessels are alternate, that is, in diagonal rows, and rarely so crowded as to give a hexagonal outline to the border. The width of these pits averages about 45 μ, while that of the pit mouth, which is narrowly elliptical, is about 30 μ (FIG. 3). Pits in transverse section show rather long and narrow canals, which widen

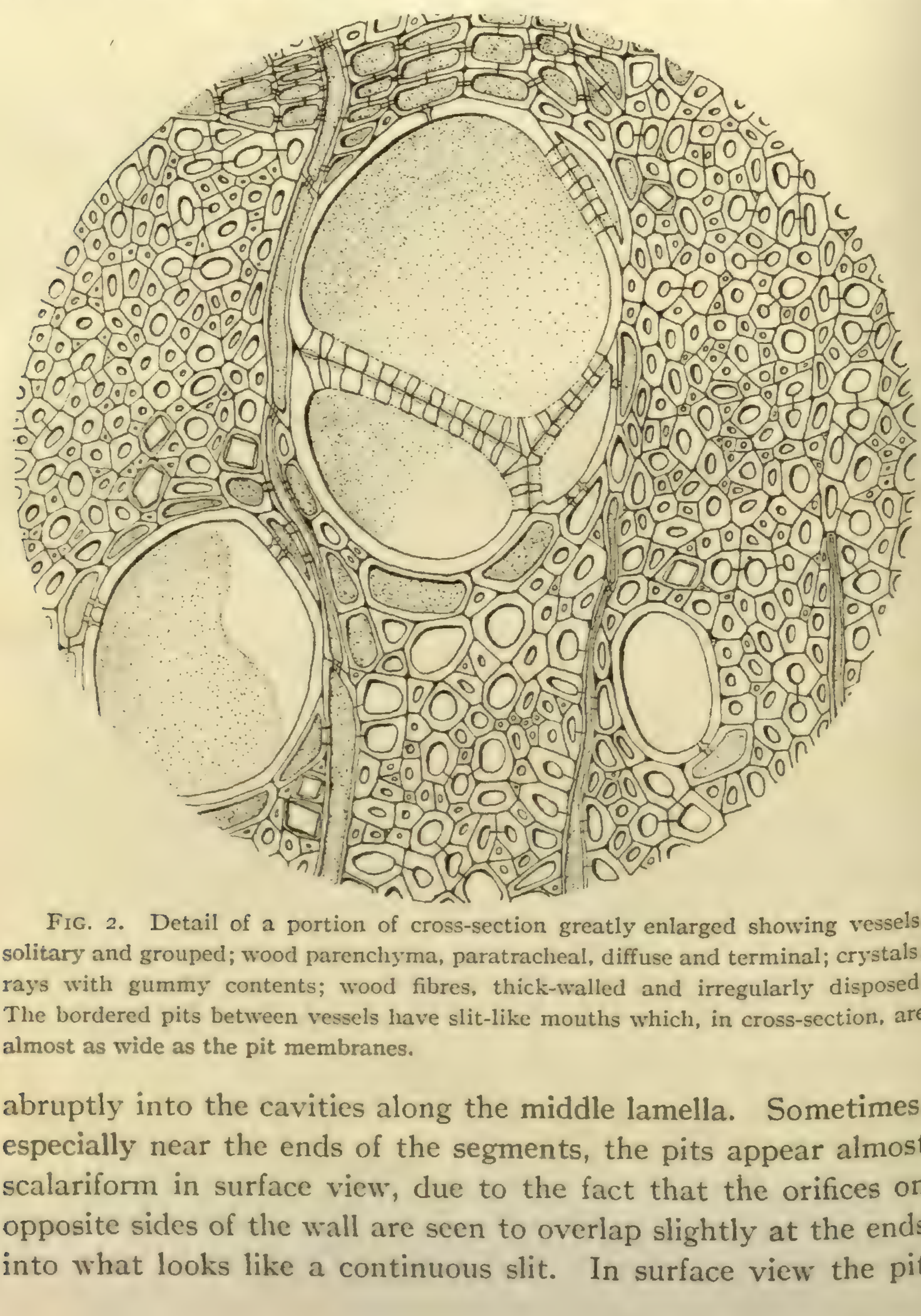

FIG. 2. Detail of a portion of cross-section greatly enlarged showing vessels, solitary and grouped; wood parenchyma, paratracheal, diffuse and terminal; crystals; rays with gummy contents; wood fibres, thick-walled and irregularly disposed. The bordered pits between vessels have slit-like mouths which, in cross-section, are almost as wide as the pit membranes.

abruptly into the cavities along the middle lamella. Sometimes, especially near the ends of the segments, the pits appear almost scalariform in surface view, due to the fact that the orifices on opposite sides of the wall are seen to overlap slightly at the ends into what looks like a continuous slit. In surface view the pit

membranes exhibit a peculiar dotted appearance quite distinct under the low power. These are due to sieve-like perforations, first described by Jönsson* in various woods of the Leguminosae and certain other families.

Tracheids.—Typical tracheids, i.e. with pointed and overlapping ends, are apparently absent. At intervals in the smallest vessels, however, it is not uncommon to find cells corresponding in every way to segments except that the ends are pitted instead of perforated. Intermediate forms with one end perforated and the other closed, except for bordered pits, are occasionally met with.

Wood fibers.—Libriform wood fibers (FIG. 4) form the ground mass of the wood. Their average length is 0.68 mm., the width of the median portion about 15 μ, and the thickness of the wall about 2.5 μ. The lumina are narrow and nonseptate. In cross section (FIG. 2) the fibers, which are polygonal in outline, appear crowded together without regular arrangement, but upon close inspection there is usually seen a fairly definite arrangement between the larger cavities (the enlarged portions of the fibers) and the smaller ones (the dove-tailing tips), due to the fact that the fibers are storied.

The pits are slit-like or narrowly lenticular, either simple or inconspicuously bordered. They are often aggregated in groups of seven to eight at the projecting "shoulder" of the fibers, midway between vertical ray tiers; see FIGS. 4 and 5. These localized pit areas, which may be seen in both longitudinal sections, serve to make the "ripple marks" more distinct. This feature has already been noted by Record† and corresponds to the condition observed by Von Höhnel‡ in a few woods, notably *Bocoa provacensis* Aubl. (*Inocarpus edulis* Forst.).

Wood parenchyma.—Wood parenchyma occurs in three arrangements: (1) as isolated strands scattered in the prosen-

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* Jönsson, B. Siebänliche Poren in den trachealen Xylemelementen der Phanerogamen, hauptsächlich der Leguminosen. Ber. Deuts. Bot. Ges. **10**: 494–513. 1892.

† Record, S. J. Storied or tier-like structure of certain dicotyledonous woods. Bull. Torrey Club **46**: 253–273. 1919.

‡ Höhnel, F. von. Ueber stockwerkartig aufgebaute Holzkörper. Sitzb. Math. Naturw. Cl. Akad. Wiss. Wien **89**: 30–47. 1884.

chymatous ground mass, i.e. diffuse; (2) as a layer surrounding the vessels, i.e. paratracheal, but not forming conspicuous masses; (3) in concentric lines or bands, two to seven (mostly two to four) cells wide, sometimes dividing into two or three closely spaced lines for greater or less distances, and apparently limiting seasonal growths; see FIG. 1.

The parenchyma strands are 0.20–0.21 mm. in length, or nearly the same as that of the vessel segments with which they

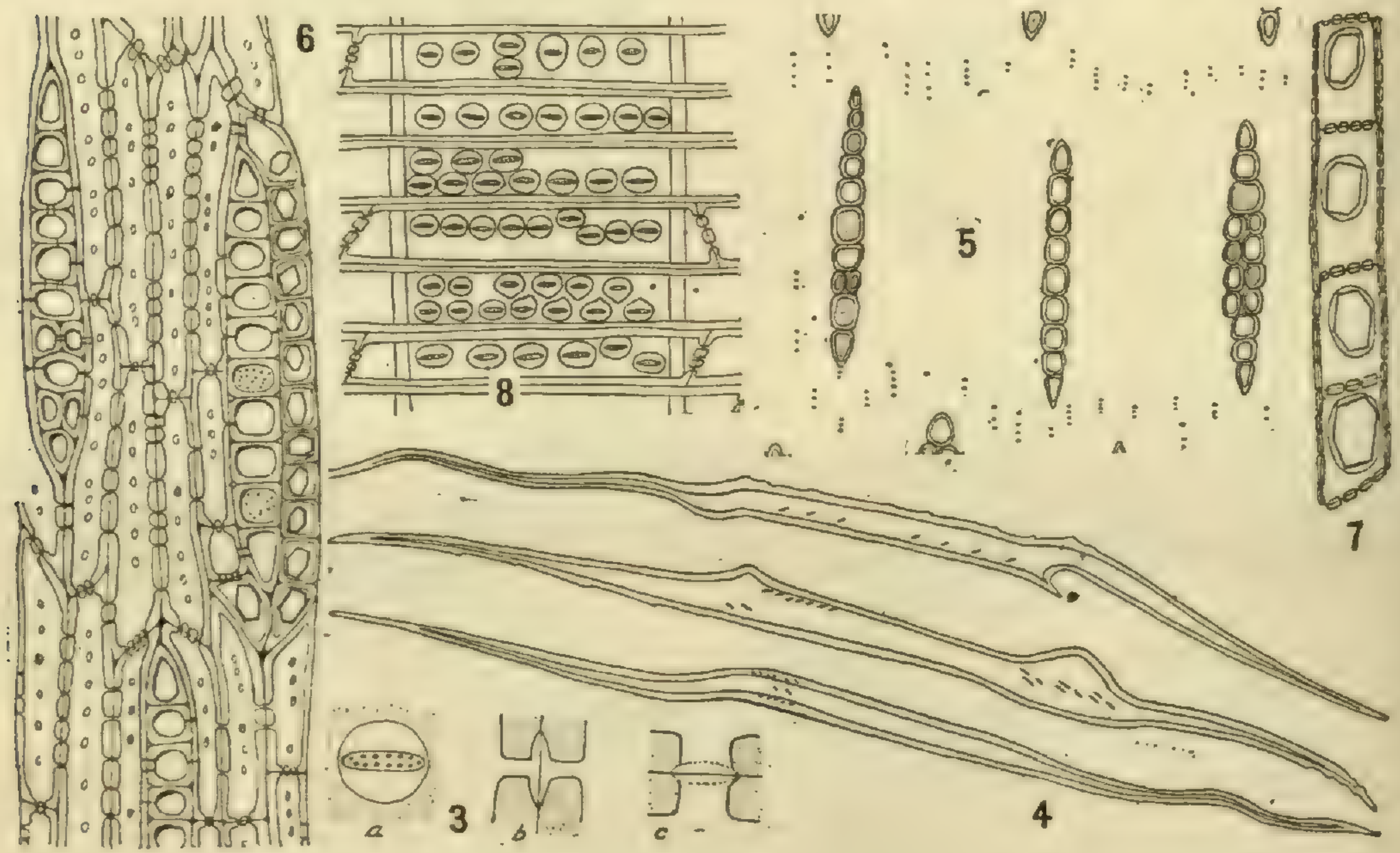

FIG. 3. Diagram of pits between vessels: *a*, surface view, showing rounded border, horizontal elongated mouth, and sieve-like perforations of pit membrane; *b*, vertical section of pit showing narrow canal, *c*, transverse section of pit showing canal almost as wide as the membrane.

FIG. 4. Various forms of wood fibers showing simple pits, which are often aggregated at the shoulders of the fibers.

FIG. 5. Sketch of tangential section showing narrow, mostly uniseriate, rays in horizontal seriation and with special pit areas between the tiers.

FIG. 6. Tangential section through terminal parenchyma, showing the rays and parenchyma strands in seriation; also chambered parenchyma with crystals.

FIG. 7. Detail of chambered parenchyma showing crystals with gelatinous covering.

FIG. 8. Radial section, showing homogeneous ray and the character of the pitting. The pits into the vessel are half-bordered and show sieve-like structure.

are in seriation. The number of cells per strand is usually two, though not infrequently three. The individual cells of the strand are not in secondary seriation (FIG. 6). The average width of a wood parenchyma cell, tangential section, is 17.5 μ; the wall is 2.5 μ thick and abundantly pitted.

Chambered parenchyma strands, with eight to fourteen crystal-bearing cells per strand, are common. The crystals (FIG. 7) are rhombohedral, measuring about 10 μ high and 7.5 μ wide. They appear to be surrounded by a gelatinous coat or layer, which may protect them to some extent from the action of nitric acid, since they are found in macerated material.

Rays.—The rays (FIGS. 5 and 6), as seen in tangential section, are in horizontal seriation, uniform, mostly uniseriate (occasionally biseriate in part), and from eight to twelve cells high. They measure 0.9–0.15 mm. in height and about 15 μ in width at the median portion.

In radial section the rays (FIG. 8) are homogeneous, and the cells are rectangular, 0.075–0.087 mm. in length and about 12.5 μ high. The marginal cells are regular in form and procumbent like the others making up the ray. The walls between adjacent ray cells are finely and abundantly pitted. The lateral walls, where in contact with vessels, exhibit numerous small bordered pits (structurally half-bordered), which are arranged in two horizontal rows, one or two to each cell. The mouth of the pit is narrowly lenticular and the membrance distintly perforated. In the heartwood the ray cells are very gummy, the gum being collected at the cross walls between cells, or along the inner side of the cell wall.

SUMMARY

1. *Machaerium Whitfordii* is a species of Colombian tree recently described by MacBride. The wood is related to the true rosewoods, appears to have good cabinet qualities, and is of commerical importance. The specific gravity of the heartwood (oven-dry) is about 1.20.

2. The wood is characterized by its very fine texture, its dark variegated color, the fine lines of terminal parenchyma, the storied arrangement of its elements (including localized pit areas on the fibers), its homogeneous and usually uniseriate rays, the presence of small half-bordered pits between vessels and ray cells, and the sieve-like perforations of the pit membrane.

Acknowledgment is made to Professor Samuel J. Record of Yale University, under whose direction this study was made, and also to Dr. Forest B. H. Brown for assistance in technique.

UNIVERSITY OF ILLINOIS.

INDEX TO AMERICAN BOTANICAL LITERATURE

1917-1919

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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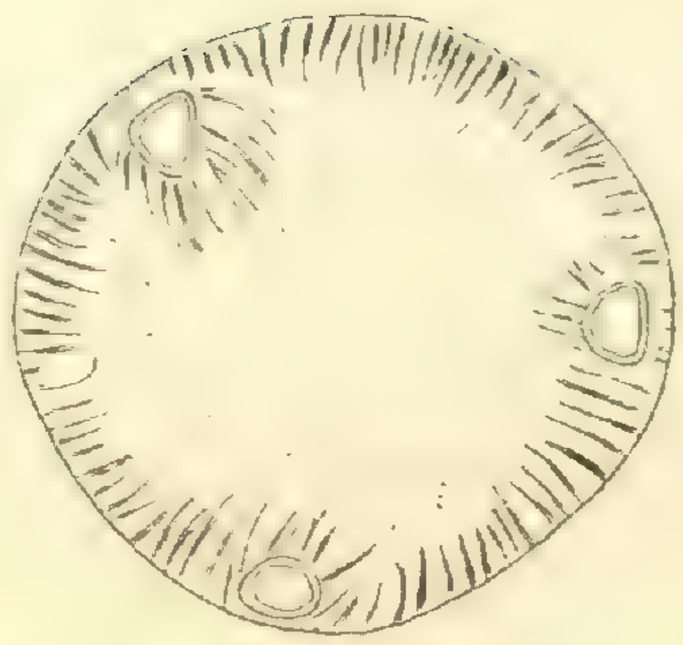

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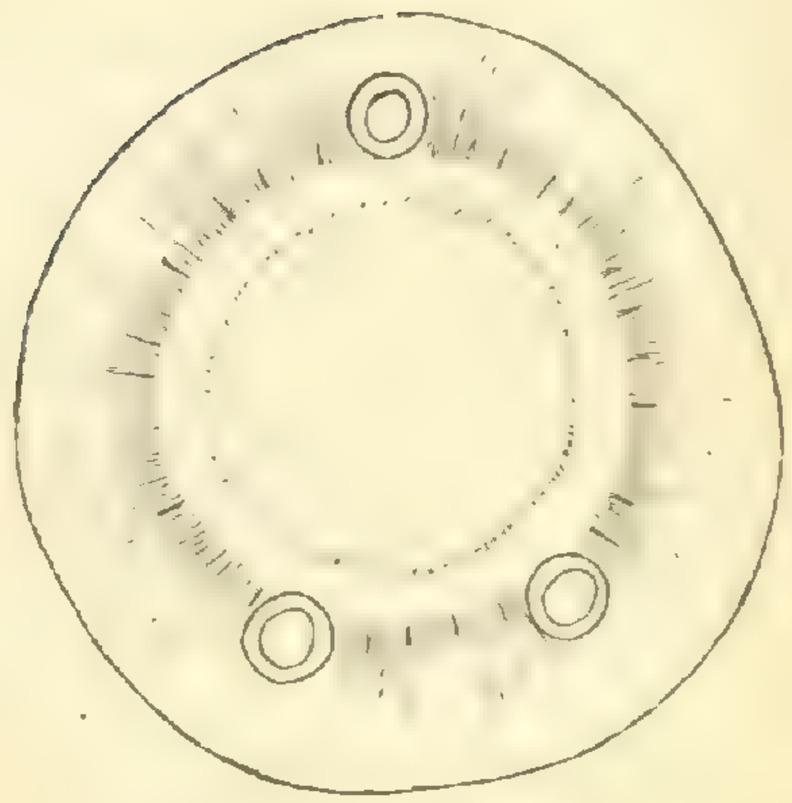

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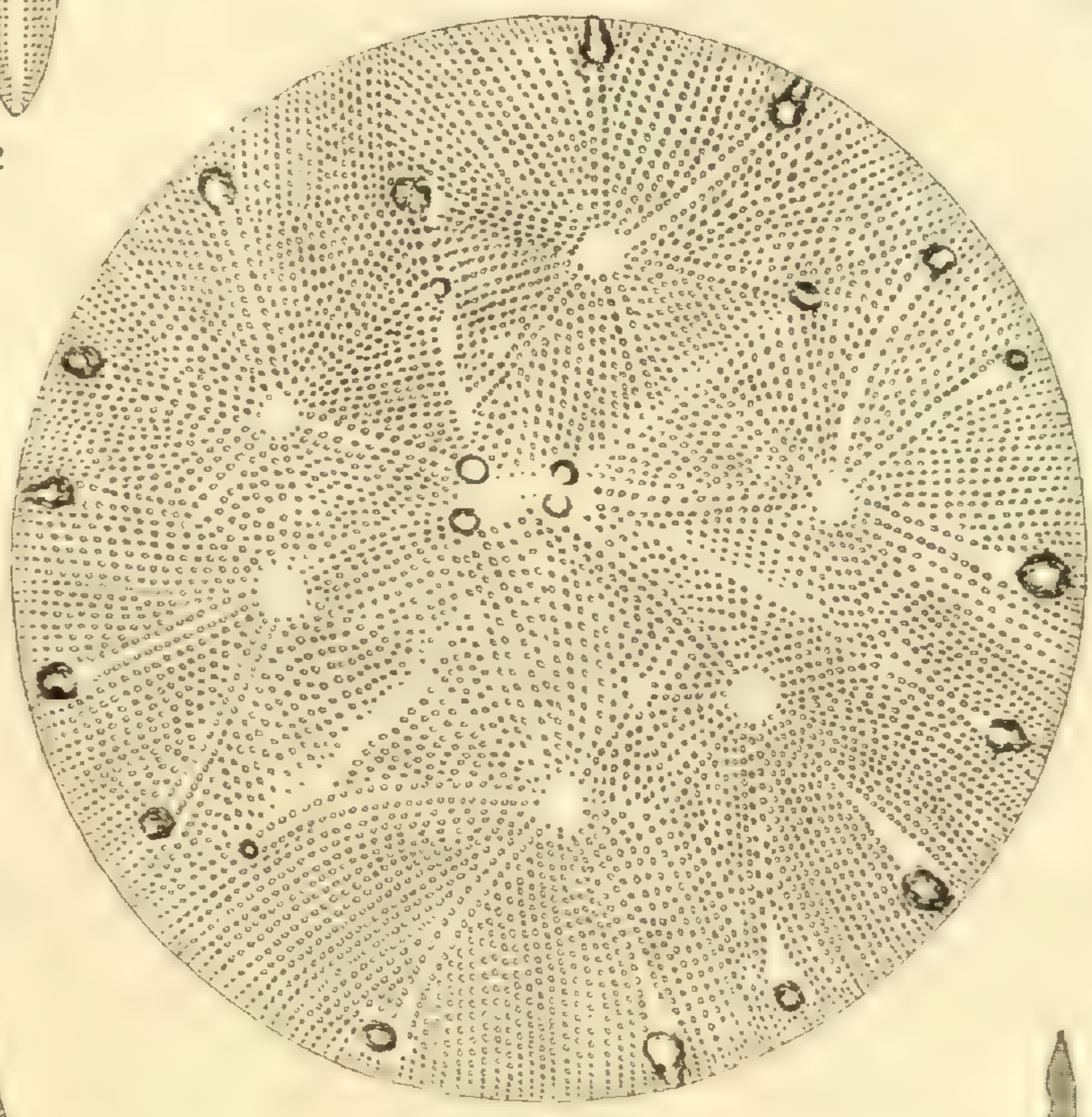

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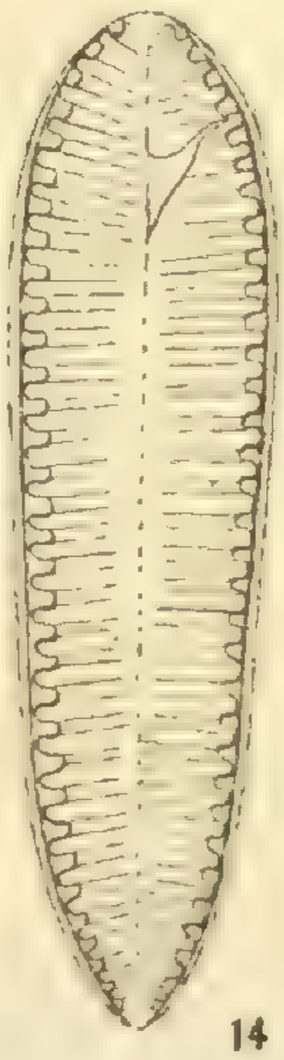

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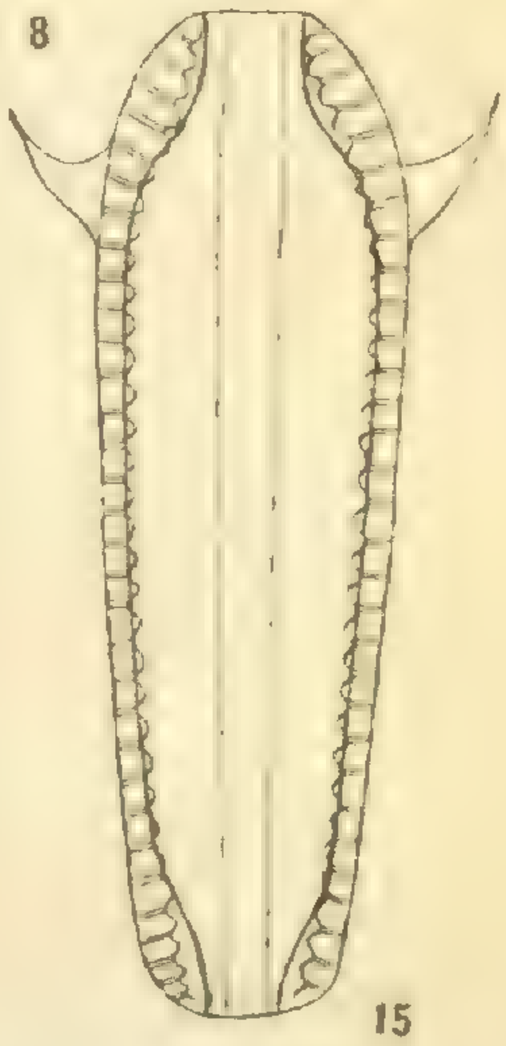

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The vegetation of Connecticut

VI. The plant associations of eroding areas along the seacoast*

GEORGE E. NICHOLS

(WITH SIX TEXT FIGURES)

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I. INTRODUCTION

This paper, with another which will appear shortly, concludes a series of articles in which the vegetation of Connecticut has been considered primarily from the standpoint of physiographic ecology.† Since the appearance of the fifth installment of the

* Contribution from the Osborn Botanical Laboratory.

† For citation of earlier papers, see list of literature at end of the present paper.

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series, the writer has published a scheme for the classification of plant associations (Nichols, '17), which differs in certain important details from that heretofore followed, although based on the same fundamental principles. For the sake of uniformity with previous numbers of the series, however, this classification will be largely neglected in the present paper. It may be of interest to note that a revised and amplified account of the vegetation of Connecticut, to be published as a bulletin by the Connecticut State Geological and Natural History Survey, is in course of preparation.

It is a familiar observation to all who visit the seacoast that the vegetation here presents many unique types of plant association. The seaweed associations of rocky shores, the associations of salt and brackish marshes and of sandy beaches and dunes—these and other distinctively seaside associations and groups of associations form the subject of this paper and of the one which follows.

At the outset, brief attention may be called to a number of important papers relating primarily to the ecology of seaside vegetation along the northern Atlantic coast, and especially to one by Kemp ('62) on "the shore zones and limits of marine plants on the north eastern coast of the United States." This remarkably clear and interesting discussion, based primarily on the study of the seaweed associations in the Casco Bay region, Maine, probably represents the first published account of a distinctly ecological nature dealing with the marine vegetation of this country, yet it seems to have escaped the notice of all the more recent writers on this subject and has but lately been brought to the writer's attention by Mr. F. S. Collins.* Among other and

* In introducing his studies, Kemp remarks: "I was aware that all the Hand Books on the Algae had noted the special localities of each species, . . . but I was not aware that in any of the books, shore lines and limits of plant growth had been made the subject of special treatment. This subject may be regarded as a minor branch of the important enquiry as to the geographical distribution of plants." Kemp divides the "tidal shore" into "six distinct zones," as follows: (1) the drift or beach zone, (2) the *Ulva* zone, (3) the *Fucus* zone, (4) the *Laminaria* zone, (5) the *Chondrus* zone, (6) the deep sea zone. The vegetation of these zones he describes in graphic detail, both from a floristic and from an ecological point of view, and in this connection ventures many suggestive observations, of which the following may serve as an illustration. Commenting on the predominance of *Ulva* in the upper portions of the intertidal region, he remarks: "A reason for this may be that the bright green color

more familiar works, Shaler's classic papers on the beaches and tidal marshes of the Atlantic coast ('85, '95, etc.), while written from the standpoint of the geologist, contain much that is of ecological interest. Kearney ('00, '01, '04) has described the seaside associations along parts of the North Carolina and Virginia shores, and has discussed the ecological relations of beach and dune plants. Shreve and Chrysler ('10) have treated the seaside associations of Maryland, Miss Snow ('02, '13) those of the Delaware coast, and Harshberger ('00, '02, '09, '11, '16, '19) those of the New Jersey coast. Transeau ('13) has described the seaside vegetation in the vicinity of Cold Spring Harbor, Long Island, and Johnson and York ('15) have made an extended study of the relation of plants to tide levels in this locality. For Massachusetts, B. M. Davis ('13) has written on the algal vegetation in the vicinity of Woods Hole, and Townsend ('13) on the sand dunes and salt marshes of the Ipswich region. Ganong ('03, '06) has described the salt and diked marshes along the Bay of Fundy and sandy beaches in northern New Brunswick, Transeau ('09) the seaside vegetation of southern Nova Scotia, and Nichols ('18) the coastal associations of Cape Breton Island, in northern Nova Scotia. In addition to these papers, the works of Penhallow ('07), Bartlett ('09, '11), C. A. Davis ('10), and D. W. Johnson ('13), while concerned primarily with botanical evidences of coastal subsidence, contain numerous observations of general or special ecological interest; and Olsson-Seffer's articles ('10) on the sand formations and sand strand floras of marine coasts, although not dealing specifically with our coast, are also worthy of note, if for no other reason than the extensive bibliographies which they contain. Complete citations for these and for other papers which are referred to in this article or in the one which follows are given in the list of literature at the end of the present paper.

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which distinguishes most of the species requires a larger amount of sunlight for its production than the olive, and red-colored plants require which inhabit lower zones and deeper water. The color of these plants of the order *Ulvaceae* which travel into deep water, is for the most part of a darker hue than those which grow in shallow places."

II. HABITAT FACTORS ALONG THE SEACOAST

The character of plant associations along the seacoast, both above and below high tide level, shows the influence of the sea in various ways and to various degrees. Some of the ways in which this influence is expressed are summed up in the following paragraphs.

A. INFLUENCES ASSOCIATED WITH SUBMERGENCE IN SEA WATER

Salinity of sea water.—This very naturally holds first rank among the factors responsible for the peculiarities of vegetation which is within actual reach of the salt water. It results primarily in the exclusion of many plants and plant associations which are present in similar situations along the shores of large bodies of fresh water, such as the Great Lakes, and in the presence of many others, notably the marine algae, which are not represented elsewhere.

The water of the open ocean in the North Atlantic contains about 3.3 per cent of salt. Along practically its entire length the Connecticut coast faces on Long Island Sound, and the salinity of the Sound water is considerably lower than that of the open ocean.* This difference in salinity is to be expected, since the Sound is partially shut off from the ocean by Long Island and has several large rivers emptying into it. The difference is of importance, because it is doubtless correlated with the absence or scarcity in many parts of the Sound of seaweeds which are abundant in similar situations along the open ocean. All intergradations are to be found along the coast and in the adjoining waters between areas in which the water is strongly saline and areas in which it is fresh, and these variations in salinity are accompanied by corresponding variations in vegetation.

The tides.—Marine algae which grow above low tide mark must be adapted to very different environmental conditions from those that grow at lower levels. For a longer or shorter period each

* According to Graves ('08) the salinity of the water in the open Sound near New Haven is about 2.8 per cent. This figure probably represents a fair average for the entire area, but of course there is considerable difference between the salt-content of the water westward from New Haven, toward the head of the Sound, and eastward, toward its mouth.

day they are exposed to the air and therefore must be able to endure, in varying degree, desiccation, exposure to rain water, and intense illumination, not to mention freezing temperatures in winter. Similarly, halophytic seed plants which grow in areas that are permanently or intermittently submerged must be able to accommodate themselves, for longer or shorter periods, to poor aëration and weak illumination. It is the varying degree to which seaweeds and seed plants are adapted to these diverse environmental conditions that in large part is responsible for the zonal arrangement of plant associations in relation to tide levels (FIG. 5), which constitutes one of the most striking features of seaside vegetation.

The range of the tides along the Connecticut coast, *i.e.*, the difference between high and low tide levels, varies greatly in different localities. The average daily range at Greenwich, toward the western extremity of the Connecticut shore line and toward the head of the Sound, is nearly three times that at New London, toward the eastern end of the shore line and just outside the entrance to the Sound. Proceeding from east to west along the Connecticut shore, the mean daily tidal ranges at various stations are: Stonington, 2.7 feet; New London, 2.5 feet; Saybrook, 3.6 feet; New Haven, 6 feet; Greenwich, 7.4 feet. As elsewhere along oceanic coasts, however, the tidal range for any given locality is not constant, but varies from time to time. The most important of these variations are seen in the semi-monthly spring and neap tides. The spring tides, occurring just after the new moon and the full moon each month, have a range from sixteen to twenty per cent greater than the average, and about twice that of the neap tides, which occur just after the first and last quarters of the moon. The equinoctial high tides, which occur at about the time of the equinoxes, rise considerably higher than the spring tides; while storm tides, especially those in which the spring tides are coincident with strong onshore gales, may rise from three to five feet higher than the mean high tide level.*

Illumination at different depths.—In proceeding from high tide mark downward into the depths of the sea there is a gradual

* For a very clear and comprehensive account of the tides and their making, see Wheeler ('06).

decrease in the amount of illumination received by plants growing on the bottom, and the intensity (or the quality) of the light at different depths is one of the most important factors controlling the distribution of many seaweeds. Taken collectively, the seaweeds of the four great natural groups of algae (the blue-greens, the greens, the browns, and the reds) differ considerably from one another in their light requirements. The blue-green and the green algae demand the greatest illumination and the red algae the least, while the brown algae are intermediate in their light requirements. The blue-greens and greens are most abundant in areas which are above low tide level; toward high tide mark they are practically the only forms present. The browns, in large part, flourish best in the regions just above and just below low tide level. The reds are most luxuriantly developed below low tide mark; in deep water they are the commonest forms. To be sure, there are numerous exceptions; certain of the red algae, under favorable conditions, range well up toward high tide mark*; certain of the green algae grow in deep water; while along our coast certain of the brown algae, viz. the kelps, are the most conspicuous members of the algal vegetation in the deeper waters. Generally speaking, however, the vertical distribution of marine algae along the coast, at least below low tide level, is closely correlated with variations in light.†

The extreme depths at which autophytic marine algae will grow depends largely on the clearness of the water. Some species have been collected, in very clear water, at depths of more than

* It is of interest, in this connection, to note that *Chondrus crispus*, one of the most characteristic of the red algae along the Connecticut coast and a species which ranges from deep water up to low tide level, frequently loses its red color completely when growing near the surface, becoming yellowish green.

† But whether it is the quantity of the light or its quality that determines the depth at which various algae will grow is a matter of dispute. To quote from B. M. Davis ('13), "The red rays of sunlight, it is claimed, cannot penetrate much below 7 fathoms, and the light at greater depths is mainly composed of blue and green rays, is feeble in yellow, and lacks red rays entirely. Certain investigators . . . hold that the quality of the light rather than its intensity determines the distribution of the green, brown, and red algae. According to this view the green algae grow under bright illumination because they require the maximum of red rays, while the red algae are able to live in deeper water because their color allows them to absorb the green rays which they especially need. The brown algae in general adjust themselves to light conditions intermediate between these extremes."

400 feet. B. M. Davis ('13) mentions twelve red algae and two browns which, in the vicinity of Woods Hole, Massachusetts, have been found growing in water from 100 to 115 feet in depth. No data are available for Long Island Sound.

Temperature of sea water.—Differences also in the temperature of the water unquestionably play an important part in determining the distribution of various marine algae, especially of forms that grow below low tide level, and the character of various associations of seaweeds may thereby be influenced to a marked degree. Thus, the dissimilarities between the algal vegetation of sheltered waters and that of more exposed waters seem to be associated in large measure with differences in temperature. Sheltered waters are warmer in summer and may be colder in winter than are exposed waters; they exhibit a much higher range of temperatures from season to season. B. M. Davis regards the temperature factor as of such fundamental significance that in classifying the sublittoral associations of the Woods Hole region he divides them primarily into two groups: the cool water sublittoral formation and the warm water sublittoral formation. The former embraces the associations of areas in which the temperature at the bottom is relatively cool during the summer months, particularly of situations which are exposed to the open sea. The latter embraces the associations of areas in which the temperature at the bottom is relatively warm during the summer months, particularly of situations which are sheltered from the open sea. Many of the seaweeds which are found only during winter and spring in the more sheltered situations flourish throughout the year in more exposed waters. The influence of differences in the temperature of the water is further seen in the pronounced seasonal periodicity exhibited by many algae. Thus, some species which are very conspicuous during winter and spring seem to disappear completely during the summer, while others, which are prominent in summer, are apparently absent in winter.

B. PHYSIOGRAPHIC INFLUENCES

Erosion and deposition.—Nowhere is the influence of erosion and deposition on the character of the vegetation more apparent than along the seacoast. Here, as elsewhere, dynamic forces of

the geologic past are in part responsible for the larger features in the landscape, but even more important in their influence are the physiographic agencies of today. The wearing away of the shore here, and its building up there, the development in exposed situations of coastal swamps, beaches and dunes—these and similar phenomena are due primarily to the activity of waves, of tidal and other currents, and, in the case of the dunes, of wind. Erosion and deposition, therefore, have an important influence on the plant associations, since the character of seaside vegetation, both above and below high tide level, bears an intimate relation to the physical nature of the substratum. Thus, the plant associations of sandy shores differ markedly from those of muddy shores, and, again, from those of rocky shores. Seaweeds, for example, are most luxuriantly developed on rocky or stony bottoms; on sandy or muddy bottoms they may be almost absent; and so on.*

Other agencies.—The influence of ice and of salt spray are further factors which may contribute materially to the character of plant associations along the seacoast. Floating ice, in addition to the indirect effect which it may exert by supplementing the abrading action of the waves, scrapes exposed rocks bare of seaweeds and in other ways affects the shore vegetation within its reach. Salt spray dashed up by waves or wind sometimes makes possible the existence of certain marine algae even above high tide mark, at the same time preventing the development here of non-halophytic land plants or at any rate having a more or less pronounced effect on their growth. The sterility in mineral nutrients of wave- and wind-deposited sand is very likely responsible, in part at least, for the peculiarities of beach and dune vegetation.

C. ATMOSPHERIC INFLUENCES

Various atmospheric agencies which tend to accelerate transpiration, especially strong winds and, during certain seasons of the year, intense heat, may affect to a marked degree the habit and structure of terrestrial plants along the seacoast. Strong illumination, likewise, may be an influential factor. The effect

* For purposes of convenience, throughout the present paper and the next one a distinction is made between *shore* and *bottom*. The application of the term shore is restricted to areas above low tide level, areas below low tide level being referred to as bottom.

of these influences is seen, for example, in the markedly xerophytic nature of the vegetation on sandy beaches and dunes; it is further reflected in the relatively xerophytic nature of the algal vegetation of the intertidal region, as compared with that of areas which are continuously submerged.

III. CLASSIFICATION OF PLANT ASSOCIATIONS ALONG THE SEACOAST

Introductory.—In a general way, the various factors which determine the distribution of plant associations along the seacoast can be summed up under two heads: (*a*) factors associated with differences in physiography, and (*b*) factors associated with differences in tide level. The physiographic influences, in the

FIG. 1. Rocky shores of the eroding type; East Haven. View, taken at about low tide, shows rockweed vegetation in lower foreground.

main, can perhaps best be grouped under two heads: erosion and deposition. Areas along the coast where the influence of currents and waves is such that erosion predominates are termed *eroding areas*. Areas where deposition predominates are termed *depositing areas*. Along an irregular coastline, such as that of southern Connecticut, eroding and depositing areas may alternate with one another in rapid sequence, erosion tending to predominate wherever there are salients in the shore-line, deposition wherever

there are reëntrants. The more important influences associated with the presence of salt water may be grouped under the head of tide levels. Roughly speaking, it can be said that the distribution in a horizontal direction of the various seaside types of plant association is determined largely by their physiographic relations,* their distribution in a vertical direction largely by their relation to tide levels. In classifying these associations, then, both sets of relations must be taken into consideration.

Plant associations grouped in relation to physiography.—With reference to their physiographic relations the plant associations

FIG. 2. Depositing shores near Watch Hill, Rhode Island; essentially similar to corresponding areas in Connecticut. Beach and line of dunes (with *Ammophila*) to right and in foreground; salt marshes in left mid-distance.

along the seacoast may be divided into two groups: *the associations of eroding shores and bottoms*, and the *associations of depositing shores and bottoms*. The essential features of an eroding shore (FIGS. 1, 3, etc.) are the presence of bluffs and headlands and the absence or sparse development of beaches, dunes and marshes. Depositing shores (FIG. 2), on the other hand, are characterized by the presence of beaches, dunes and marshes, and by the ab-

* This generalization applies strictly only along the shores of the open Sound, since of course differences in the salinity of the water also affect the horizontal distribution of the plant associations where the salty waters of the sea meet the fresh waters of inflowing streams.

sence of bluffs and headlands. Eroding bottoms, as a rule, are rocky, stony, or shelly; depositing bottoms are muddy or sandy. So significant are these physiographic differences that in the detailed account which follows the plant associations have been grouped primarily with reference to their physiographic relations, their relation to tide levels being used as a secondary means of subdivision.

Plant associations grouped in relation to tide levels.—With reference to the relation of the substratum to tide levels, three regions may be distinguished: the *littoral*, the *sublittoral*, and the *supralittoral*. The limits of these regions have been variously described by different writers;* as used in the present treatment they may be defined as follows. The littoral region comprises that part of the shore which lies between mean low tide level and mean high tide level. The sublittoral region extends from mean low tide level (the lower limit of the littoral) downward and seaward as far as the maximum depth at which the higher algae grow. The supralittoral region extends from mean high tide level (the upper limit of the littoral) upward and landward as far as the character of the vegetation is definitely associated with the proximity of the sea.

Corresponding approximately with these regions, the plant associations of the seacoast can be divided into three groups. The littoral region is characterized by associations of plants which are adapted to endure alternate daily submergence by tidal waters and exposure to the air; the sublittoral region by associations of plants which are adapted to endure continuous submergence; and the supralittoral region by associations of plants which are

* By derivation, the term *littoral* (used both as a noun and as an adjective) means simply "of or pertaining to the seashore," and in this sense the word has often been used more or less indiscriminately with reference to plants or plant associations occurring anywhere along the seashore. Technically, and particularly in ecologica literature, this term has come to be used somewhat more strictly, but, even so, its application in practise has been far from uniform. Three recent writers, for example, have used it in as many different ways. Johnson and York ('15) define the littoral in the sense in which it is used in the present paper; B. M. Davis ('13) describes it as "the zone extending from low water mark to the highest point at which marine algae cease to grow;" while Transeau ('13) seems to embrace in the littoral all areas, both below and above low tide level, which are "occupied by the shore drift in transit." The terms sublittoral and supralittoral likewise are capable of various interpretations (see discussions by Sumner, Osburn and Cole, '13, B. M. Davis, '13, and Johnson and York, '15).

adapted to endure continuous exposure to the air. The characteristic plants of the supralittoral region are terrestrial seed plants; those of the sublittoral are marine algae, together with a few aquatic seed plants; while the plants of the littoral include both seed plants of terrestrial derivation and algae of marine derivation. But while, broadly speaking, these three groups of plant associations are very distinct from one another, it is rarely possible to draw sharp lines of demarcation between them. The principal reason for this is obvious, namely, the recurrent fluctuations in the height of the tides. Thus, in the upper levels of the sublittoral region there is an area which ordinarily is submerged at low tide, but which is uncovered by the semi-monthly spring low tides; and the vegetation here naturally includes elements which are more characteristic of the littoral region above than of the sublittoral. Similarly, in the lower levels of the supralittoral region there is an area, ordinarily exposed, but flooded by the spring tides, in which the vegetation may differ quite markedly from that of areas which are never submerged. The equinoctial tides, storm tides, and wave-dashed spray likewise may exert a modifying effect on the character of the associations in the supralittoral.

In some ways it might seem desirable to group the plant associations of the seacoast primarily with reference to tide levels, treating their physiographic relations as of secondary importance. Such a grouping, however, would not be in harmony with the larger physiographic scheme of classification which embraces, not alone the associations of the seacoast, but all other types of vegetation in Connecticut as well.*

IV. THE VEGETATION OF ERODING AREAS AND ITS ECOLOGICAL RELATIONS

A. ROCKY SHORES AND BOTTOMS†

1. Seaweed associations of the sublittoral region

Introductory.—The sublittoral region can be divided into two fairly well-defined "sub-regions": the *upper sublittoral* and the

* This is essentially the scheme used by Transeau ('13) and by Johnson and York ('15).

† With reference to the physical character of the surface acted upon by the waves, two general types of eroding shore can be distinguished along the Connecticut coast:

lower sublittoral. The former includes the bottom between low tide mark and a depth of from four to six feet; the latter includes all of the sublittoral below this depth. The vegetation of both these zones, on rocky, stony or shelly bottoms, consists wholly of marine algae, except as there may be an occasional sparse growth of eel grass. Essentially all of the seaweeds to be mentioned in the lists which follow are attached forms: in large part they find a foothold on rocks, stones, or shells; but many of them, particularly among the smaller species, also grow as epiphytes on other seaweeds, or on eel grass. No account whatever is taken here of the vast assemblage of microscopic free-floating algae which constitute what is known as the plankton, nor of the various attached forms included among the diatoms. In the discussion of the seaweed associations which follows, the published works of Hall ('76), Farlow ('79), Collins ('00, '05), B. M. Davis ('13), Transeau ('13), and Johnson and York ('15) have been freely drawn upon, and the lists of species have been checked over by Mr. F. S. Collins, whose published lists of marine algae (*op. cit.*) have been followed in matters of algal nomenclature.

Associations of the lower sublittoral.—By far the greater number of seaweeds characteristic of the lower sublittoral region belong to the red algae, while the green algae are practically absent here. The brown algae are represented by comparatively few species, but among these are the kelps, particularly *Laminaria Agardhii*, which are conspicuous by their large size, individual plants often acquiring a length, along our shores, of ten or more feet. Little of a definite nature can be stated with regard to the grouping into associations of the algae in the lower sublittoral, and many of them are seldom seen, except as washed ashore during storms. Some of the larger species, however, frequently form extensive beds.* Most of the species characteristic of the lower sublittoral

(*a*) *eroding rock shores*, where the substratum consists of firmly compacted rock, *i.e.*, of rock in the ordinarily accepted sense; and (*b*) *eroding drift shores*, where the substratum consists of glacial drift, which technically may be classed as uncompacted rock. The general description which follows applies more particularly to rock shores and bottoms, but attention will be directed later to resemblances and differences between the vegetation here and that along eroding drift shores.

* Regarding the associational relations of the algae of the littoral and sublittoral regions in the vicinity of Woods Hole, B. M. Davis ('13) remarks that "groups of species may cover large areas and even form broad zones of vegetation . . . but

grow best in strongly saline waters bordering the open ocean, and in Long Island Sound they develop much more luxuriantly eastward, toward the entrance, than westward, toward the head of the Sound. In general, there is little question that the algal vegetation of the lower sublittoral is much more poorly developed along the Connecticut shore than, for example, in the Woods Hole region. A list of species characteristic of the lower sublittoral in this region is given below, but while all of these are known to be more or less abundant in Long Island Sound, sufficient data are not available to permit generalizations regarding their relative frequency.*

BROWN ALGAE (*Phaeophyceae*)

Chorda Filum	CW	*Laminaria Agardhii*	CW
Cladostephus verticillatus	CW	*Laminaria digitata*	C
Desmarestia aculeata	CW	*Sargassum Filipendula*	W
Desmarestia viridis	CW		

RED ALGAE (*Rhodophyceae*)

Agardhiella tenera	CW	*Hildenbrandtia Prototypus*	CW
Ahnfeldtia plicata	CW	*Lomentaria uncinata*	W
Antithamnion cruciatum	CWZ	*Phyllophora Brodiaei*	CW
Ceramium rubrum	CWZ	*Phyllophora membranifolia*	CW
Ceramium strictum	WZ	*Plumaria elegans*	C
Ceramium tenuissimum	WZ	*Polyides rotundus*	CW
Champia parvula	W	*Polysiphonia elongata*	CW
Chondrus crispus	CW	*Polysiphonia nigrescens*	CW
Corallina officinalis	CW	*Rhodymenia palmata*	CW
Cystoclonium purpurascens	CW	*Rhodomela Rochei*	CW
Dasya elegans	WZ	*Seirospora Griffithsiana*	WZ
Delesseria sinuosa	C	*Spermothamnion Turneri*	CW
Griffithsia Bornetiana	W	*Spyridia filamentosa*	WZ
Grinnellia americana	CW		

Associations of the upper sublittoral.—Many seaweeds of the lower sublittoral commonly range upward to low tide level. The so-called Irish moss (*Chondrus crispus*), for example, a flat-fronded, purplish red species with pronounced dichotomous

the vegetation more often consists of small and more scattered groups, the limits of which are generally more easily recognized and in which a single species usually predominates." These groups he terms associations. For the Woods Hole region he distinguishes nearly sixty such associations or groups of associations.

* The letters C and W, placed after various species in this and the following list, are taken from B. M. Davis ('13). They indicate respectively species which, in the Woods Hole region, he includes in the cool-water or in the warm-water sublittoral formation. The letter Z indicates species which he includes in the *Zostera* formation, to be treated by the writer in the paper which will follow this one.

branching, which sometimes grows in water more than a hundred feet deep (in the Woods Hole region) and which is a characteristic component of the lower sublittoral flora, probably nowhere develops more luxuriantly than in the upper sublittoral, where it commonly occurs in great profusion on exposed rocks just below low tide mark. Another form which is prominent in this zone, as well as in the lower sublittoral, is *Ceramium rubrum*, a profusely branched, bright red, filamentous species. This plant probably has a more ubiquitous distribution along the Connecticut coast than any other red alga. Still another red of the lower levels which thrives in the upper sublittoral is *Hildenbrandtia Prototypus*, a species which forms conspicuous reddish incrustations over rock surfaces. In fact, there are probably few algae of the deeper waters which, under favorable conditions, do not range upward to low tide level at certain seasons of the year, and some of them, e.g., *Ceramium* and *Hildenbrandtia*, may extend upward locally well into the littoral region.

But the outstanding feature of the vegetation in the upper sublittoral is the presence of certain seaweeds which do not occur in deep water, or which develop most prolifically near the surface. Especially characteristic are certain green algae, viz., *Bryopsis plumosa* and various species of *Cladophora*; certain browns, e.g., *Ectocarpus* spp., *Pylaiella littoralis*, and *Phyllitis fascia*; and certain reds, e.g., *Nemalion multifidum* and various species of *Callithamnion* and *Polysiphonia*. Indeed, it seems not unlikely that the scarcity near the surface of many of the red algae of deeper waters is due in large measure to their inability to compete successfully with these other species which thrive so luxuriantly in this region. Taken as a whole, the plant population of the upper sublittoral comprises an intimate admixture of green, brown, and red algae, but with the reds numerically the strongest. Locally and at different seasons of the year various associations and groups of associations can be distinguished, and, in particular, various of the species already mentioned as characteristic of the upper sublittoral commonly form conspicuous masses of vegetation. A list of algae characteristic of the upper sublittoral in Long Island Sound is given below. Some of these are restricted to these upper levels, particularly among the greens and browns; but

many, among them most of the reds, range to much greater depths.

GREEN ALGAE (*Chlorophyceae*)

Bryopsis plumosa	W	*Cladophora gracilis*	CWZ
Chaetomorpha Linum	CW	*Cladophora lanosa*	W
Cladophora albida refracta	CW	*Cladophora rupestris*	CW
Cladophora arcta	W	*Ulva Lactuca*	

BROWN ALGAE (*Phaeophyceae*)

Castagnea virescens	WZ	*Phyllitis fascia*	
Chorda Filum	CW	*Punctaria latifolia*	
Chordaria flagelliformis	CW	*Pylaiella littoralis*	W
Ectocarpus confervoides	CWZ	*Ralfsia clavata*	CW
Ectocarpus siliculosus	CWZ	*Sargassum Filipendula*	W
Leathesia difformis	CW	*Scytosiphon lomentarius*	
Mesogloia divaricata	W	*Sphacelaria cirrhosa*	W

RED ALGAE (*Rhodophyceae*)

Antithamnion americanum	W	*Gracilaria multipartita*	W
Callithamnion Baileyi	WZ	*Grinnellia americana*	CW
Callithamnion roseum	WZ	*Hildenbrandtia Prototypus*	CW
Callithamnion tetragonum	W	*Lomentaria uncinata*	W
Ceramium rubrum	CWZ	*Melobesia pustulata*	CW
Ceramium strictum	WZ	*Nemalion multifidum*	
Champia parvula	W	*Polysiphonia fastigiata*	W
Chondria dasyphylla	WZ	*Polysiphonia fibrillosa*	W
Chondria tenuissima	W	*Polysiphonia urceolata*	C
Chondrus crispus	CW	*Polysiphonia variegata*	W
Corallina officinalis	CW	*Polysiphonia violacea*	CW

2. Seaweed associations of the littoral region

Introductory.—The vegetation of the littoral along eroding rocky shores, like that of the sublittoral, is composed of seaweeds; but the ecological relations of the seaweeds growing in these two regions are very dissimilar.* In comparison with the strictly hydrophytic species of the sublittoral, the characteristic seaweeds of the littoral are relatively xerophytic. As in the case of the sublittoral region, however, the vegetation of the littoral is by no means uniform throughout and, with reference primarily to vegetational dissimularities, this region likewise can be divided into two "sub-regions": the *lower littoral* and the *upper littoral*.†

* See earlier discussion of these relations, pp. 99, 100.

† Along depositing muddy shores, as will be seen later, sharply defined differences in the character of the vegetation at different levels clearly differentiate the area here termed the lower littoral into two parts, designated by Johnson and York

The boundary between these two subdivisions lies approximately at the average level of neap high tides, or a little below, but it varies locally and, in favorable situations, the vegetation of the lower littoral may extend well up toward mean high tide mark.

Associations of the lower littoral.—The characteristic plants of the lower littoral along eroding shores are the rockweeds, *Ascophyllum* and *Fucus* (FIGS. 3 and 4). These conspicuous olive-brown seaweeds grow in massive profusion and commonly plaster

FIG. 3. Granitic eroding shore at low tide, showing dense growth of *Ascophyllum* and *Fucus* in the littoral region; East Haven.

over almost completely with their coarse, leathery, forked fronds the surfaces of rocks, occurring also, though perhaps less luxuriantly, on piles and other woodwork. The two may grow intermixed, or one or the other may predominate locally. *Fucus* usually ranges somewhat nearer high tide mark than *Ascophyllum*, and along rocky shores the upper limit of the lower littoral may be regarded as coinciding approximately with the upward limit of

('15) the *lower littoral* and the *midlittoral*. A similar subdivision can be made along other types of shore (as Johnson and York have done), but the vegetational dissimilarities here are much less apparent and for this reason the writer has chosen, excepting along depositing muddy shores, to include in the lower littoral all of the mean intertidal region below the upper littoral.

range for this plant. Locally, however, the rockweeds are scarce or absent, and it is mostly in areas of this description, or as epiphytes on the rockweeds, that the various other algae listed below occur. *Chaetomorpha*, *Rhizoclonium*, and *Scytosiphon*, however, commonly grow in tidal pools. The following seaweeds may be regarded as characteristic of the lower littoral.

GREEN ALGAE (*Chlorophyceae*)

Bryopsis plumosa
Chaetomorpha spp.
Enteromorpha clathrata
Enteromorpha intestinalis
Rhizoclonium spp.
Ulva Lactuca

BROWN ALGAE (*Phaeophyceae*)

Ascophyllum nodosum
Ectocarpus spp.
Fucus platycarpus
Fucus vesiculosus
Phyllitis fascia
Pylaiella littoralis
Ralfsia clavata
Scytosiphon lomentarius

RED ALGAE (*Rhodophyceae*)

Ceramium rubrum
Ceramium strictum
Hildenbrandtia Prototypus
Nemalion multifidum
Polysiphonia fastigiata
Porphyra laciniata

Some of these species, it will be noted, are also characteristic of the upper sublittoral, and in deep tidal pools still others of these sublittoral algae may be represented, but it is seldom that any of them range far above low tide mark.* Aside from the rockweeds, perhaps the most conspicuous algae of the lower littoral are *Phyllitis* and *Porphyra*, although the sea lettuce, *Ulva Lactuca*, is sometimes prominent.

Associations of the upper littoral.—The chief factor in limiting the upward extension of the rockweeds and other seaweeds that are found in the lower littoral, but not in the upper, is dessication. Along perpendicular sea walls which are protected from intense illumination these plants reach higher levels than along shores where they are exposed to strong sunlight. The drying effect of air and sun throughout much of the upper littoral is commonly so great that between tides the seaweeds growing here become to all appearances completely dried out and frequently the more delicate forms become baked tight to the rock surface. Very few marine

* Locally, almost any of the species here listed as characteristic of the lower littoral may range downward below mean low tide mark. This is true, for example, of both *Ascophyllum* and *Fucus*.

algae can endure such extreme conditions and largely for this reason the algal vegetation at the higher levels is very much impoverished: in fact, along many rocky shores there is practically no vegetation toward high tide mark. The red algae are frequently represented in the upper littoral by the relatively xerophytic *Bangia fusco-purpurea*; but the browns, except for species that may inhabit tidal pools or which may occasionally push their way up from the lower littoral, are absent. The characteristic algae of this zone are certain greens, particularly, species of *Enteromorpha* (FIG. 4). The two species of this genus listed for

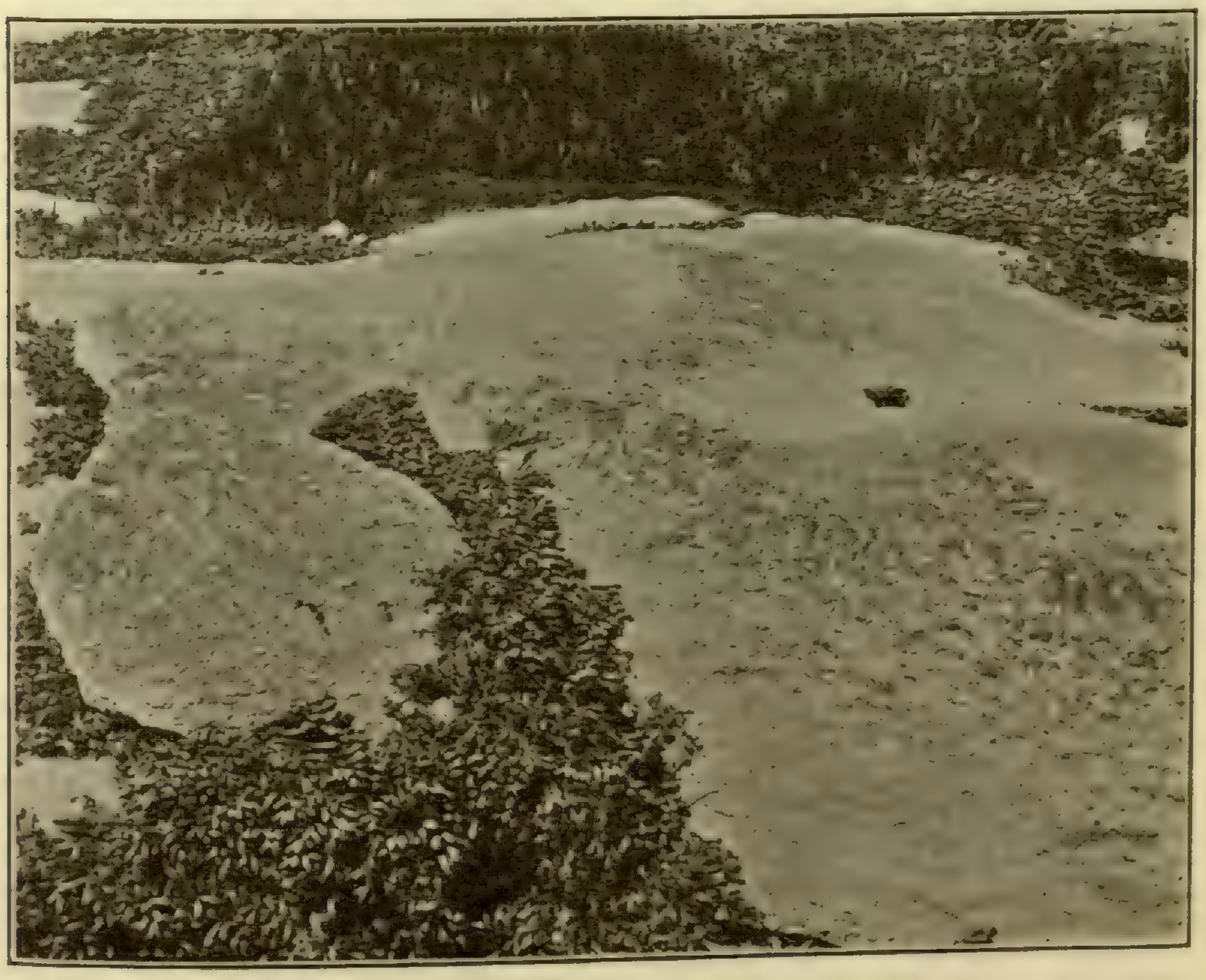

FIG. 4. *Fucus* and *Enteromorpha* on granitic shore; East Haven. The *Enteromorpha* appears as a dark streaking on the otherwise bare rock surface.

the lower littoral (*E. clathrata* and *E. intestinalis*) may occur in the upper littoral as well, but there are two other species of this genus, viz., *E. minima* and *E. prolifera*, which apparently are restricted to this region. In addition to the enteromorphas, the following algae frequently are represented more or less abundantly in the upper littoral: (greens) *Urospora penicilliformis*, *Rhizoclonium* spp., *Ulothrix* spp.; (blue-greens) *Calothrix* spp.

3. Associations of the supralittoral region

The associations of rocky sea bluffs.—Like the sublittoral and the littoral regions, the supralittoral (FIG. 5) can be divided into a lower and an upper "sub-region." The *lower supralittoral* comprises a belt immediately above mean high tide mark in which, except frequently for an impoverished growth of *Enteromorpha* spp., the rock surface is practically destitute of vegetation of any description. Conditions here are too dry for seaweeds and too salty for lichens and mosses, while the development of halophytic seed plants is prevented primarily by the mechanical action of waves and ice in times of heavy sea. This plantless belt varies in width: along the more exposed shores it may extend upward for a distance of twelve or fifteen feet; in less exposed situations it may be quite narrow.

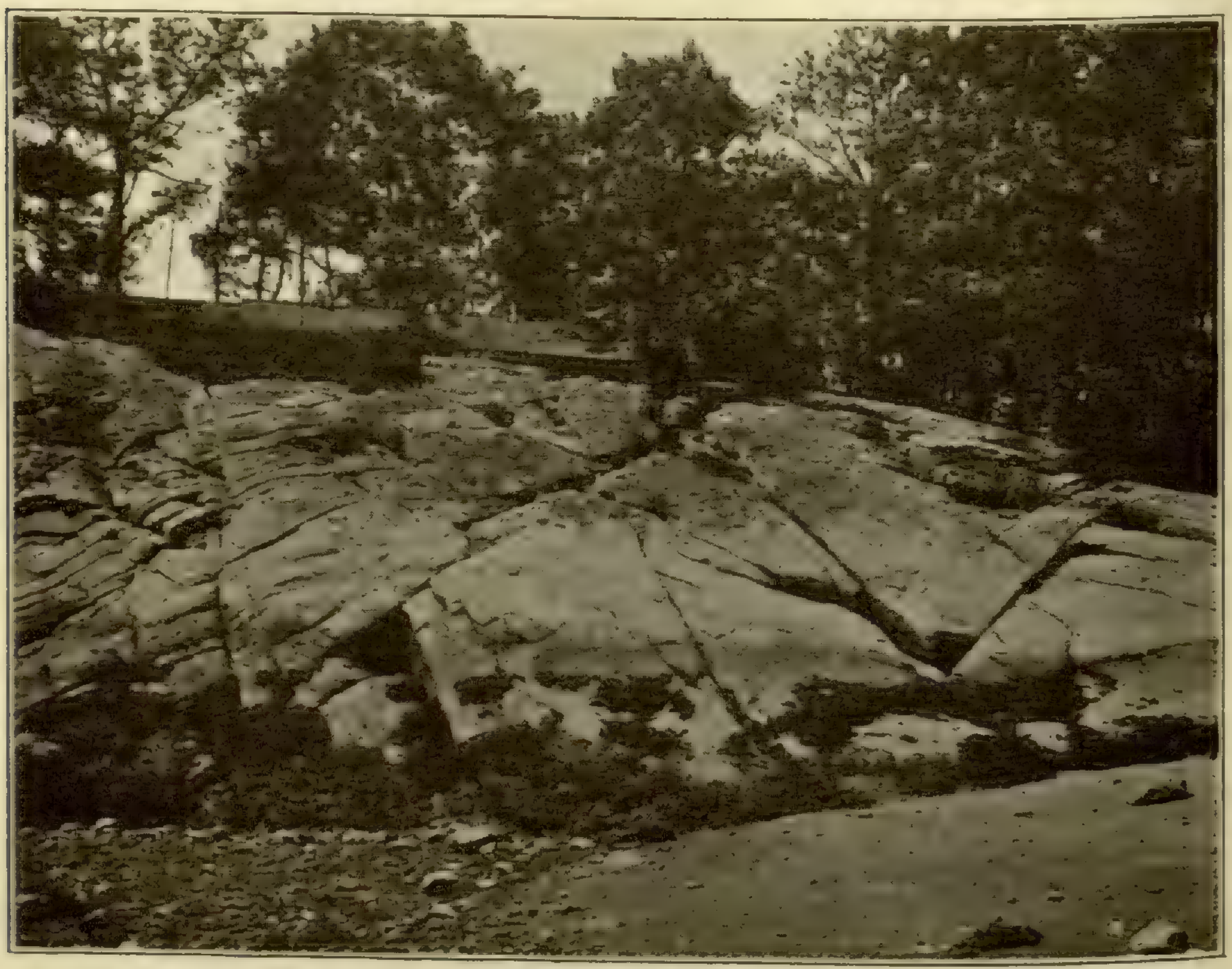

FIG. 5. Zonation of plant associations along a rock-bound shore; East Haven. The following zones are apparent, from below upward: (1) *Fucus* and *Ascophyllum* of lower littoral; (2) *Enteromorpha*, etc., of upper littoral; (3) plantless lower supralittoral; (4) lichen-moss zone of upper supralittoral, with seed plants above.

The *upper supralittoral* extends from the upper edge of the

lower supralittoral upward and away from the water to where the influence of the sea virtually ceases. The vegetation here consists, primarily, of various rock-face and crevice lichens. Sometimes there is a more or less distinct lichen-moss zone just above the plantless region, but, as a rule, the crevices at any rate support, even here, a limited assortment of vascular plants. Prominent among these latter, especially in the more exposed situations, are various more or less halophytic species: such, for example, as *Carex silicea*, *Juncus Gerardi*, *Lathyrus maritimus*, *Prunus maritima*, *Plantago decipiens*, and *Solidago sempervirens*. Other characteristic plants of the upper supralittoral along rocky shores are listed below.

Juniperus virginiana
Deschampsia flexuosa
Danthonia spicata
Poa compressa
Poa pratensis
Festuca rubra
Festuca octoflora
Smilacina stellata
Smilax glauca
Myrica carolinensis
Rumex Acetosella
Sagina procumbens
Pyrus arbutifolia atropurpurea
Amelanchier sp.
Rosa humilis
Rhus typhina
Rhus Toxicodendron
Psedera quinquefolia
Hypericum gentianoides
Opuntia vulgaris
Gaylussacia baccata
Anagallis arvensis
Achillea Millefolium
Chrysanthemum Leucanthemum

It will be noted that, except for *Sagina*, all of the plants here mentioned are xerophytic, light-requiring species. Indeed, aside from the presence of the halophytic element, the associations of the upper supralittoral along the seacoast differ but little from the pioneer associations elsewhere developed on ordinary rocky uplands. Toward the upper edge of the supralittoral region there commonly occurs a dense thicket of bayberry, sumac, poison ivy, and various others of the shrubs and vines listed.

B. SHORES AND BOTTOMS OF GLACIAL DRIFT

1. Associations of the sublittoral region

The associations of stony bottoms.—Where the substratum acted on by the forces of erosion is glacial drift, most of the finer detritus commonly is carried away by the currents, leaving behind on the bottom the boulders formerly present in the drift but too heavy to be transported. This type of bottom is a common one along exposed parts of the Connecticut shore line, yet little need be

said regarding its vegetation, since it is essentially similar to that of rocky bottoms. As a rule, the boulders are more or less scattered, and between them, in areas protected from erosion by the boulders themselves, the bottom is sandy. The vegetation in such places resembles that of depositing sandy bottoms, to be described in a later paper.

2. Associations of the littoral and supralittoral regions

Eroding shores of glacial drift compared with rocky shores as an environment for plants.—Even along a rock-bound coast the influence of waves and ice on the character of seaside vegetation is very apparent; but, as compared with the conditions along shores of glacial drift, their influence there is relatively inconsequential. Along rock shores the influence of these physiographic agencies on plants is direct, and it is confined to areas within actual reach of the waves. Along shores of glacial drift their indirect influence may be even more important; for here the undermining and abrading effect of the waves, dashing against the soft, uncompacted rock, not only influences the vegetation within reach but that at higher levels as well. The contrast is quite analogous to that pointed out elsewhere in comparing rock ravines with ravines in glacial drift.*

Associations of the supralittoral.—Wherever deposits of glacial drift are exposed to wave action, the natural result of the washing away of the soil on vegetation is the partial or complete destruction of whatever plant associations may happen to have been present. Associations along the entire face of an eroding bluff may thus become completely annihilated, so that, in extreme cases, the bluff will be virtually barren of vegetation of any description. But, as a rule, plants are not entirely absent here. For the forces of erosion are most active during winter and early spring, which is a period of inactivity for plants; during the growing season there is practical freedom from erosion. In consequence, even an actively eroding bluff may support a scattered population of plants, mostly annual species which are able to mature between successive periods of erosion; and, on bluffs

* See Nichols, '16, p. 237, etc. Also, in this connection, compare Cowles's description of the conditions on eroding clay bluffs along Lake Michigan (Cowles, '01, p. 50 et seq.).

where the periods of erosion are separated by periods of years, perennial herbs and shrubs may become established.

The vegetation of eroding bluffs in glacial drift usually includes, in varying abundance, various of the herbaceous xerophytes elsewhere listed as characteristic of rock bluffs (see list on p. 109), together, commonly, with such additional species as *Equisetum arvense*, *Polygonum scandens*, *Oenothera muricata*, *Apocynum cannabinum*, *Verbascum Thapsus*, *Ambrosia artemisiifolia*, and *Solidago lanceolata*. It may also include, especially below, such distinctively seaside plants as *Lathyrus maritimus*, *Cakile edentula*, and *Solidago sempervirens*. In addition to this, in the main, essentially pioneer flora there usually are present various relicts of the preëxisting vegetation, especially plants which formerly grew toward the top of the bluff and have survived on raft-like clumps of earth that have slid down the slope (i.e., "*slump plants*").

In the lower supralittoral, between ordinary high tide level and the base of an eroding bluff, as a rule, there is a narrow fringe of stony, gravelly, or sandy beach. The vegetation here resembles that of the corresponding region on shingle and sandy beaches, to be described later.

Associations of the littoral.—Along the base of an eroding bluff of glacial drift, the littoral region ordinarily is occupied by a rather steep, stony beach, built up out of boulders and stones of all sizes which have been washed out of the bluff itself. The vegetation here, though ordinarily less well developed (as in the area illustrated by FIG. 6), is essentially similar to that of the littoral along rocky coasts, except that frequently there is an incursion of associations characteristic of depositing shores, favored by the protection from wave activity which the boulders afford. Thus, it is not unusual here to find incipient salt marshes developed here, in among the boulders of the littoral (FIG. 6).

C. FOREST GROWTH ON UPLANDS ADJOINING THE SHORE

Along the relatively sheltered Connecticut coast the vegetation of sea bluffs and headlands is much less distinctive than along very exposed coasts, such as that of northern Cape Breton (see Nichols, '18, p. 319 et seq.), and the influence of the sea on the character of

the forests and forest trees near the shore is much less marked. It is only occasionally here that trees are encountered which exhibit the weather-beaten, one-sided aspect so familiar along more exposed coasts, and the forests immediately adjoining the shore may differ but little from forests developed in similar situations inland. There is a general tendency, however, for these forests to

FIG. 6. Eroding shore with stones and boulders derived from glacial drift (seen above) which formerly covered entire area; East Haven. Miniature salt marsh in foreground; also, in foreground, outcrop of granite exposed by removal of drift.

be relatively open and somewhat xerophytic. On many of the small rocky islands which occur scattered along parts of our coast, for example, the forest is made up largely of pitch pine (*Pinus rigida*), and the bulk of the undergrowth consists of the shrubs which have been listed as characteristic of the upper supralittoral along rocky shores (see p. 109). On some of these islands an appreciable difference can be observed between the forest growth of windward and lee slopes (assuming the effective winds to blow from off the sea). On one of the larger and more primitive of the Thimble Islands, for example, the prevailing type of vegetation is an open forest, predominantly pitch pine, but with a scattering of hickory (*Carya* spp.), black oak (*Quercus velutina*), sassafras (*Sassafras variifolium*) and red maple (*Acer rubrum*), and with the undergrowth as described above. On lee slopes,

however, the forest is less open; beech (*Fagus grandifolia*), basswood (*Tilia americana*), red oak (*Quercus rubra*), and chestnut (*Castanea dentata*) are common; and the undergrowth includes witch hazel (*Hamamelis virginiana*) and mountain laurel (*Kalmia latifolia*), elsewhere absent.

D. SUCCESSIONAL RELATIONS ALONG ERODING COASTS

Successional changes in the character of plant associations along the seacoast result primarily from changes in physiography, and where the physiography is essentially stable for long periods of time the vegetation likewise, except for seasonal variations, may remain practically unchanged. Thus, along an eroding rocky coast, the arrangement of the seaweed associations into definite zones in relation to tide levels has no successional significance: this arrangement, of itself, is scarcely less permanent than are the tides. In the upper supralittoral along the coast, as on rocky uplands elsewhere, there is an undoubted tendency for the vegetation to become more mesophytic, but the extent to which any such changes can actually take place is pretty definitely limited by edaphic factors.

Along eroding coasts in glacial drift, however, the conditions are quite different from those along rocky coasts. Here, owing to the unstable nature of the substrata acted on by the waves, changes in topography may be brought about with comparative rapidity. The catastrophic influence of such changes on the preëxisting vegetation, elsewhere described (p. 110), may be looked upon as in the nature of a retrogressive succession. Once established, the pioneer vegetation of an eroding bluff may maintain virtually the same aspect year after year, or just as long as the bluff continues to be acted on, at more or less frequent and regular intervals, by the agencies of degradation. But should erosion cease, due to the accumulation of boulders along the base of the bluff or to the formation of some other protective barrier, then the universal tendency of vegetation everywhere to approach the mesophytic condition becomes at once apparent. A bluff, formerly populated by a scattered assemblage of weeds and other herbaceous xerophytes, may thus become covered with a grassy turf or with a dense thicket of bayberry, sumacs, poison ivy and the like. In many

cases, so favorable are the soil moisture relations along sea bluffs of glacial drift that the vegetation of slopes protected from wave action includes such more or less hydrophytic forms as *Salix cordata*, *Alnus rugosa*, *Rosa carolina*, *Heracleum lanatum*, *Verbena hastata*, and *Sambucus canadensis*.

There is one other phase of succession along the seacoast that may well be suggested here. The courses of the currents, which in large measure determine the nature of the bottom in different areas and, *ipso facto*, the nature of the vegetation growing on the bottom, are by no means constant in their direction and influence. For example, through the development of a sand spit, a strong tidal current may become deflected into an entirely new channel, thereby subjecting what formerly were depositing areas to erosion, and vice versa. Similarly, the development of an off-shore barrier beach may result in an eroding shore becoming transformed into a depositing shore. The importance of such changes in relation to vegetation is self-evident.

SHEFFIELD SCIENTIFIC SCHOOL,
YALE UNIVERSITY.

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The diecious nature of buffalo-grass*

JOHN H. SCHAFFNER

The buffalo-grass, *Bulbilis dactyloides* (Nutt.) Raf., was apparently first described by Nuttall in 1818 from a staminate specimen and named *Sesleria dactyloides*. In 1855, Steudel named the carpellate form *Antephora axilliflora* and, in 1859, Engelmann described the buffalo-grass as a diecious plant under the name of *Buchloë dactyloides*.

The species was usually regarded as diecious until in recent years some authors have described it as a peculiar type of monecious grass. Plank,† in 1892, asserted that the grass was monecious. He says: "During one of my botanical rambles in Kansas, while walking over soil newly moved by a freshet, I noticed the peculiar appearance of the individual plants of buffalo grass growing upon it. There were scores of them, if not hundreds. All of them appeared to be seedlings, having yet not sent out stolons. All of these plants were monœcious." Plank thought that the stolons proceeding from sexually different parts of the plant each reproduced its own form. And it is true, from what appears below, that any given stolon will produce only staminate or only carpellate inflorescences. The main question is as to the original nature of the seedlings. In 1895, Hitchcock‡ also described a single specimen he had raised from seed as monecious. He says that a few seeds were germinated in the greenhouse, that a single seedling was transferred to an out door plot, that this plant bloomed in two years, and that both carpellate and staminate flowers were present.

Among the recent manuals the following statements appear: J. K. Small, 1903, Flora of the Southeastern United States—"Spikelets dioecious"; N. L. Britton, 1904, Manual of the Flora of the Northern States and Canada, second edition—"A perennial

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* Papers from the Department of Botany, The Ohio State University, No. 114.

† Plank, E. N. *Buchloe dactyloides*, Englm., not a diœcious grass. Bull. Torrey Club **19**: 303–306.

‡ Hitchcock, A. S. Note on buffalo grass. Bot. Gaz. **20**: 464.

stoloniferous monoecious or apparently dioecious grass"; A. S. Hitchcock in Gray's New Manual of Botany, seventh edition, 1908—"Seedlings are monoecious, but the staminate and pistillate branches propagate their own kind"; J. M. Coulter and A. Nelson, 1909, New Manual of Botany of the Central Rocky Mountains—"Spikelets dioecious (rarely monoecious), very unlike"; Britton and Brown, 1913, An Illustrated Flora of the Northern United States, Canada and the British Possessions, second edition—"A perennial stoloniferous monoecious or apparently dioecious grass."

The writer has been intimately acquainted with buffalo-grass since childhood and had always regarded it as diecious until he read the statements in the recent manuals. Recently the problem of its true nature became of interest because of its possible use in experiments on the nature of sex in the higher plants. It was thought that a plant which began its life by developing both staminate and carpellate branches and then continued these branches with but one type of sexual expression might yield some interesting results when placed under experimental control. But, as will appear below, this expectation was not realized because buffalo-grass is a diecious species under normal conditions, and the writer has not succeeded in his attempt to induce a monecious character under abnormal conditions, as he has with certain other plants.

FIELD OBSERVATIONS

During the summer of 1919, field observations were made at Morganville, Clay County, Kansas. Because of abundant rains in the spring, especially in June, the buffalo-grass bloomed very profusely and the season was unusually favorable for the study. In this region the typical prairie consists largely of *Andropogon scoparius* Michx. and *A. furcatus* Muhl. The buffalo-grass is usually in small sharply defined areas, often forming a nearly pure stand or containing one or more species of *Bouteloua*. On large normal areas there is often a space a yard or more wide which is purely carpellate or purely staminate, but many areas have the staminate and carpellate inflorescences rather closely and uniformly intermingled.

Areas were chosen for study which, in the memory of the writer,

had been cultivated fields, entirely devoid of buffalo-grass, and which had later been abandoned. A ravine filled deep with the wash of surrounding fields was also studied.

1. A small abandoned field much tramped by cattle. There were three small, pure, staminate patches and three small, pure, carpellate patches. No mixed patches were found.

2. An abandoned field, now in pasture, in which patches of buffalo-grass have become established. The patches were as follows:

Carpellate patches		Staminate patches	
No. of patches	Diameter	No. of patches.	Diameter
1	9 ft.	1	8 ft.
1	7 "	1	6 "
1	6 "	1	5 "
3	3 "	2	4 "
		1	3 "

In this field not one case of mingled inflorescences was found. All the patches were pure and were mostly blooming abundantly, some patches being entirely covered with inflorescences. It is probable that each of these patches originated from a single seed.

3. A pasture ravine filled with a deep layer of soil washed from surrounding fields. The new-formed soil was covered with weeds and Kentucky blue-grass and here and there small patches of buffalo-grass had developed. These were mostly over three years old and had probably gained a foothold in this usually rather wet soil because of the very dry seasons of 1917 and 1918. Most of the patches probably developed from seed, although it is possible that detached stolons may have been washed down from hillside patches, or carried in the feet of cattle. Seventeen isolated patches were found in the ravine. There were ten purely carpellate and seven purely staminate. In no case was such a small patch found to have both staminate and carpellate inflorescences.

4. An abandoned field of several acres turned into a pasture, after being sown to tame grasses. Patches of buffalo-grass, some of considerable size, were numerous. They were either of pure stand, staminate or carpellate, or mixed. The mixed patches sometimes had the carpellate and staminate inflorescences commingled, or were staminate in one part and carpellate in another. The patches observed are tabulated below:

Pure carpellate		Pure staminate		Mixed	
No. of patches	Diameter	No. of patches	Diameter	No. of patches	Diameter
1	10 ft.	1	12 ft.	*1	12 ft.
1	8 "	2	10 "	*1	10 "
2	7 "	3	8 "	1	9 "
3	6 "	2	7 "	*1	8 "
3	5 "	3	6 "	1	7 "
1	4 "	2	5 "	*1	6 "
2	3 "	5	4 "	1	4 "
2	2 "	2	3 "	1	2 "
		2	2 "		
3	1 "	1	1 "		
18		23		8	

* Patches marked with a star had the staminate and carpellate inflorescences in distinct areas.

Of the forty-nine patches found in this field, therefore, forty-one were pure (eighteen carpellate and twenty-three staminate) and only eight were mixed. Of the mixed, four were generally commingled and four had the carpellate and staminate inflorescences in distinct parts of the patch. Presumably the mixed patches originated from more than one seed, although the possibility remains that they represent the vegetative offshoots of a monecious organism.

5. A patch of mixed stand of special interest. One patch was of unusual character and deserves special consideration. It was about 16 ft. long and 6 ft. wide; one end, about 5 ft., was pure staminate; the middle, about 5 ft., was pure carpellate; and the other end, about 6 ft., was pure staminate. On either side of the carpellate patch, where it bordered on the staminate ends, there was a mixed zone of staminate and carpellate inflorescences about a foot wide. This patch has evidently originated from three separate patches side by side, which have but recently been united by vegetative expansion.

EXPERIMENTAL RESULTS

Previous to the field observations taken the past summer, as stated above, seed was collected by the writer during the summer of 1917, in Clay County, Kansas, and after being carefully prepared so that not more than one grain would be in a "husk," was planted in the autumn on shallow benches in the

botanical greenhouse. Later, single individuals were transferred to pots, great care being taken to see that each plant in a pot represented a single seedling. The pots were placed in a bed in the greenhouse some distance apart and the plants made a good growth during the summer and autumn of 1918. They put out abundant stolons and began to bloom early in the spring of 1919. While the plants were in the greenhouse, five of them bloomed and all were pure in sexual expression. There were three pure carpellate plants and two pure staminate plants. On May 28, 1919, these five plants, together with eleven others in pots, were transplanted out of doors. These plants made a remarkable growth and all of them bloomed before the end of the summer. Of the eleven plants which bloomed out of doors, five were carpellate and six staminate. There were, therefore, exactly eight carpellate plants and eight staminate plants. None showed any signs of moneciousness. Two other plants in pots were kept in the greenhouse but have not bloomed up to the present time. The evidence from these sixteen plants, each grown from a single seed, is conclusive that *Bulbilis dactyloides* is strictly a diecious plant, and if intermediates, or monecious individuals, ever occur, either through the influence of environment or by a mutation, they are to be looked upon in the same light as other intermediates which occur in many normally diecious species.

The writer has no evidence whatever that a monecious form exists, but if there are specimens that show staminate and carpellate inflorescences on the same stolon or that show staminate and carpellate stolons coming without question from the same individual, the fact of a monecious form can be readily determined. The writer has shown elsewhere* that maleness or femaleness, as expressed in the sporophyte of the Anthophyta, is frequently reversed, and such a reversal is, of course, theoretically possible in the buffalo-grass. If Hitchcock's plant was monecious, it may have been such an accidental intermediate. It is possible, however, that two seedlings may have been mistaken for one

* Schaffner, John H. The expression of sexual dimorphism in heterosporous sporophytes. Ohio Jour. Sci. **18**: 101–125. 1918.

—— The nature of the diecious condition in *Morus alba* and *Salix amygdaloides*. Ohio Jour. Sci. **19**: 409–416. 1919.

—— Complete reversal of sex in hemp. Science II. **50**: 311–312. 1919.

unless especial care was taken to separate the individual grains from the hardened glumes. Because of the rapidity of growth and the great length of the stolons one can also readily make mistakes as to the limits or origin of individuals in the field. There is nothing in Plank's account which is entirely conclusive as to the nature of the plants he observed. The very fact that it is stated that each stolon produces its own kind would in itself throw doubt on the supposition that the plants observed were monecious. Plank made the statement, "there are probably a thousand individuals of the staminate form to one of the pistillate." This is not true of the seedlings, which according to my experiments and observations are about equally divided into staminate and carpellate individuals. In the field the one kind of inflorescence is about as abundant as the other. By superficial observation one might, however, get the notion that the staminate inflorescences were greatly in the majority, since the staminate stalks are comparatively tall and conspicuous while the carpellate are short and usually hidden among the leaf blades. In walking over a large patch of the grass, one might see very few carpellate inflorescences unless he got down on his hands and knees, especially if the grass had not been pastured. The buffalo-grass is holding its own well under civilized conditions and toward its eastern limit is spreading in the pastures and abandoned fields because its strongest competitors, *Andropogon scoparius* and *A. furcatus*, are much more subject to destruction through grazing and tramping of live stock.

Unreported ferns from Montana

PAUL W. GRAFF

The state of Montana is located in such a position that it has not been adequately covered by any of the botanical "Manuals." In fact the work of botanical collectors has been more one of surrounding the state than of covering it. Coulter and Nelson's "New Manual of Rocky Mountain Botany" overlaps somewhat from the south, Piper's "Flora of the State of Washington" and Howell's "Flora of Northwest America" overlap from the west, and Bergman's "Flora of North Dakota" together with Britton and Brown's "Illustrated Flora" overlaps, to a less extent, from the east. The result is that, as the first four of these are comparatively local in the area covered, many Montana species have been entirely omitted from them. Their compilers have only mentioned the state of Montana incidentally to the discussion of the spread of species beyond the area under consideration. Rydberg's "Flora of Montana," published as Volume 1 of the Memoirs of the New York Botanical Garden, is a very comprehensive check list, although many of the very common species are not mentioned. This is due to the fact that it was based on a few scattered but large collections made on summer collecting trips. The fern list, although not complete, is fairly extensive, thanks to the very able collecting of R. S. Williams. Rydberg's more recent "Flora of the Rocky Mountains and Adjacent Plains" adds three fern species, previously unreported from the state, namely, *Asplenium Filix-foemina* (L.) Bernh. var. *cyclosorus* Rupr., *Polystichum munitum* (Kaulf.) Presl, and *Botrychium simplex* Hitchc. Why the first of these has remained so long unreported is hard to say as it is one of the most common of ferns to be met with along the mountain streams of western Montana, localities similar to those in which the typical form of the species is found. The second and third of the additions seem to be of rare occurrence each, so far as the writer is aware, being known from but one collection.

P. munitum was collected on Mount Aeneas in the Swan Range by D. T. MacDougal in 1901, and *B. simplex* Hitchc., by R. S. Williams at Columbia Falls in 1905. Well-preserved specimens from both these collections are in the herbarium of the University of Montana, and it seems strange that further collections of these species have not been made.

In glancing through the herbarium of the University of Montana, and that of the University of Montana Biological Station, the presence was noted of five ferns which, as yet, remain unreported from the state. Four of these belong to the Polypodiaceae, and the remaining one to the Ophioglossaceae. Though all of these are found in the western and mountainous portion of the state, four of the five are not reported by Coulter and Nelson for any part of the Rocky Mountain region. Three, moreover, are not to be found in Piper's manual. The addition of these five to those already known increases the total number of species and varieties of Montana pteridophytes to thirty-five, only two less than Piper reports for the state of Washington, and seven more than Coulter and Nelson attribute to the whole Rocky Mountain region.

1. OPHIOGLOSSUM VULGATUM L. Sp. Pl. 1062. 1753.

FLATHEAD COUNTY: Flathead Lake, Yellow Bay, August, 1916, *A. W. L. Bray;* July 1, 1917, *P. W. Graff 1280*, with young and immature sporangia; July 25, 1917, *P. W. Graff 1397*, a collection of mature specimens. The three collections were made at about 888 meters elevation.

These are the only collections of this rare fern which are known from Montana. They were made in the vicinity of the University of Montana Biological Station, at Yellow Bay on Flathead Lake, the second and third collections having been made along the margin of a meadow which is flooded during the season of high water, although surrounded by forest. During the months of May and June this meadow is a shallow pond to the forest border, but during the dry month of July it becomes an open field. The fern was found under the shadow of the overhanging branches of aspen and alder among the grass which had sprung up as the water receded. Numerous small patches were found on all sides of the meadow so that, in

this locality, it might almost be called abundant. In many instances there was associated with it the grape fern, *Botrychium silaifolium* Presl. This latter species, however, tended to grow farther into the forest, and was not confined to the grassy margin. The collection of the *Ophioglossum* is doubly interesting, since it seems to have escaped detection in the other Rocky Mountain states.

2. CYSTOPTERIS FRAGILIS (L.) Bernh. var. ANGUSTATA (Hoffm.) Luers. Farnpfl. 459. 1889.

GALLATIN COUNTY: vicinity of Bozeman, Mystic Lake. August 10, 1905, *J. W. Blankenship 637*, on cliffs at an altitude of 1800 meters.

This delicate variety is represented by but one collection in the herbarium of the University, although the typical form of the species is a very common fern throughout the western portion of the state, growing on rocky soil and in rocky crevices up to an altitude of about 3,000 meters. So far as I have been able to ascertain, the variety has not been reported from any of the region surrounding Montana. The specimen cited is as large as the typical form of the species, but the frond is much thinner and the pinnules are more toothed and finer-pointed. The following specimen in the herbarium of the University tends very strongly to approach this variety. Flathead County, vicinity of Bigfork, July 21, 1908, *M. E. Jones 9739*, at an elevation of 900 meters.

3. ASPIDIUM CRISTATUM (L.) Sw. Schrad. Jour. Bot. 1800[2]: 37. 1801.

FLATHEAD COUNTY: vicinity of Rost Lake, July 6, 1901, *D. T. MacDougal 668*, at an elevation of 975 meters.

This is the only collection of the crested shield fern from Montana, so far as known, two very good specimens being in the herbarium of the University of Montana. When further collections have been made, however, it seems probable that it will be found growing in the Glacier Park region, as well as in the Mission and Swan Mountains, if not further to the south and east.

4. ASPIDIUM FILIX-MAS (L.) Schrad. Jour. Bot. 1800[2]: 38. 1801.

GLACIER NATIONAL PARK: vicinity of Blackfoot Glacier, August 30, 1909. *M. E. Jones*. FLATHEAD COUNTY: north shore of Flathead Lake in the vicinity of Bigfork, July 20, 1908, *M. E. Jones 9720*, near the lake shore to the south of the town, at an elevation of about 888 meters. MISSOULA COUNTY: Mission Mountains, Lake Angus McDonald, June 23–24, 1901, *D. T. MacDougal 367*, on the shore of the lake at an elevation of 1,000 meters.

While indefinitely reported as found scatteringly through the western states, I have been unable to locate any definite report of this species from Montana. Rydberg, in his "Flora of Montana," reports it on hearsay but gives no record of any collection or collector. It seems to have been collected only in the mountainous western portion of the state, and there only to have been found sparingly. In the vicinity of Bigfork, at the northern end of Flathead Lake, it is locally abundant on the low lake shore. At the upper end of Lake Angus McDonald, under the dense shade of a grove of immense specimens of *Thuja plicata* D. Don, the giant cedar, and along the stream which feeds the lake, is a considerable bed of this fern. The species has been reported also from St. Mary's Lake (Sinyaleamin) in the Mission Mountains, and from several localities in the Bitter Root Valley, but I have seen no specimens from these places.

5. ASPIDIUM SPINULOSUM (O. F. Müller) Sw. var. INTERMEDIUM (Muhl.) D. C. Eaton; A. Gray, Manual, ed. 5, 665. 1867.

GLACIER NATIONAL PARK: Lake McDonald, August 25, 1909, *M. E. Jones*, at 950 meters elevation.

While the var. *dilatatum* (Hoffm.) Hook. has been reported previously from both Missoula County and to the northward, and the species proper from the Glacier Park region, the var. *intermedium* has remained unreported and has, so far as known, been collected but once. Both the species proper and this variety seem to be extremely rare in Montana.

The following table shows graphically the known distribution, in Montana and the surrounding states and provinces, of the five species enumerated in this paper, together with the three mentioned

in the introduction. It is evident that certain of these species should be found in those localities to the north and south of Montana, where similar mountainous conditions exist.

	Wash-ington	Oregon	Idaho	Wyoming	Colorado	North Dakota	South Dakota	Montana	British Columbia	Alberta
BOTRYCHIUM SIMPLEX				×	×			×	×	×
OPHIOGLOSSUM VULGATUM								×		
CYSTOPTERIS FRAGILIS var. ANGUSTATA								×		
POLYSTICHUM MUNITUM		×	×					×		
ASPIDIUM CRISTATUM			×			×		×		
ASPIDIUM FILIX-MAS		×	×		×		×	×	×	×
ASPIDIUM SPINULOSUM var. INTERMEDIUM			×					×		
ASPLENIUM FILIX-FOEMINA var. CYCLOSORUS	×		×					×	×	×

DEPARTMENT OF BOTANY,
UNIVERSITY OF MONTANA,
MISSOULA, MONTANA

INDEX TO AMERICAN BOTANICAL LITERATURE

1918–1919

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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BULLETIN

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Inheritance of sugar and starch characters in corn

R. A. HARPER

(WITH PLATES 3–5)

The mass of the evidence accumulated in the last decade from the most widely varied material, both plant and animal, certainly indicates that judged by visible appearances for many cases at least the old question as to whether widely separated and heritably fixed types can be connected by finely graded intermediate forms has been settled in the affirmative. In view of the vast number of observations and experiments which have been made it is worth while not to lose sight of this positive result in the still existing conflict of rival theories. Such series of connecting links have been produced experimentally under rigidly controlled conditions by Castle, Jennings and others. It is still urged, however, that this apparent continuity of variation in visible characters is not a true index of what is occurring in the germ plasm. The old dogma of the fixity of specific types has been revived as a dogma of the fixity of the germ plasm. The units of the germ plasm, genes, factors, etc., it is urged, must be conceived as definite and unvarying except for special and rather cataclysmic alterations at relatively infrequent intervals.

The range of evidence as to continuity of variation covers all the common types of reproduction both sexual and asexual. To refer only to the most significant papers which have appeared we may note that such series of connecting links between widely diverse end products have been produced by Castle and Phillips

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('14) with hooded rats reproducing sexually and with inbreeding, by Jennings ('16) with *Difflugia* and by Hegner ('19) with *Arcella* reproducing asexually by simple cell division. Stout ('15) has also shown that such series can be produced by bud variation in *Coleus* and that by selection of these bud variants for specific leaf patterns races of purity and constancy sufficient for successful commercial uses can be produced. The facts as to the occurrence of widely divergent mutants or sports, which may or may not be monstrosities, and their fixity in heredity are in just about the same position as they were when Darwin concluded that such sporadic variations have probably not played any very significant rôle in evolution. The discovery that such forms as *Oenothera gigas* may have a tetraploid chromosome number is highly interesting and may indicate a possible method of effective evolutionary change, but the great mass of what have been more recently called mutants we are coming to realize are merely the extremes of series of fluctuating variants. There is adequate evidence, it seems to me, that such fluctuating changes may involve the fundamental constitution of the cells and may be expressed in chromosome changes as well as in gross characters. The discovery that forms may vary by a single chromosome is apparently established for *O. lata*. Kuwada ('11, '15 and '19) has claimed also, without however giving very adequate evidence, that the sugar corns vary in the number of their chromosomes from nine to twelve (haploid number) and that the sugar corns may have a larger number of chromosomes than the starchy corns. Such data are of great interest, but Kuwada's figures are not very convincing as he gives no full series of the stages for any one race. He lists nine varieties with which he worked. Four starchy races are reported as showing ten chromosomes (haploid number), one sugar corn as showing nine to ten and nine to twelve, respectively (haploid numbers). In his 1919 paper he attempts to utilize these observations in drawing conclusions as to the hybrid ancestry of corn.

As I pointed out ('12), in the recent genetical studies practically the first advance beyond the simple concepts that every visible character of a plant is due to, and transmitted by, a simple fixed factor which remains unchanged, except for certain rather rare and deep-seated changes resulting in mutations, was toward a theo-

retic provision for greater complexity in breeding results than these simple hypotheses allowed. Among Mendelians as well as others there is now coming to be rather general agreement that visible characters are due to several or even numerous more or less independently modifiable or varying units in the germ plasm. This change of viewpoint is due to the increasing number of cases which show more complicated results from crossing individuals differing in a single visible character than are provided for in the so-called monohybrid formula. The visible data in many such cases are a large number of individuals in the F_2 which do not show the character in question in sharply differentiated form, that is, the occurrence of intermediates as the older authors would have described them.

It has been universally shown by the actual data that in crossing sweet corns with flints in certain cases at least intermediate kernels appear in the F_2 which are not so plump as flints and not so wrinkled as a good quality of sugar kernels, but there has been a general tendency to disregard these facts in the interest of maintaining simple Mendelian expressions for the results of such crosses. Whether there are any races in which these intermediates do not appear is not altogether clear.

Sturtevant ('99) reports three varieties of what is apparently a similar intermediate type of corn, based on three ears sent him from the San Padro Indian collection of Dr. Palmer. He proposes the binomial *Zea amyleasaccharata*, "Starchy-sweet corn," for such types and states that he also obtained kernels of similar appearance from Peru in 1895. Sturtevant describes all these types as having the upper portion of the kernel sweet and the lower portion starchy, an interesting special case in the intergrading of these characters. Collins and Kempton ('13 and '14) believe that in the offspring of crosses between sweet and waxy varieties irregularities in the expected Mendelian ratios are due to a "failure of some sweet seeds to develop a wrinkled exterior." Correns ('01) made the investigation of the starch and sugar characters one of the main objects of his classic study of heredity in corn and has recorded his observations of the degree of wrinkling of the kernels in the F_1 and F_2 generations with considerable completeness. But Correns's conclusions and interpretations have

been more widely quoted than his actual data. He tested two sweet races, his No. III *R. caerulaeodulcis* and No. VI *R. dulcis*, both of which he describes as constant. The seed was obtained from Haage and Schmidt and both races are described by Koernicke ('85). The total number of crosses between sweets and flints and pops where only one kind of pollen was used was twenty-one. Eighteen were between flint and sweet races and two were between pop and sweet races. One involved the doubtful pop race *R. nana*. In five cases he reports as smooth or almost smooth the kernels in the F_1 from crosses of flints and sweets, but states without very detailed comparisons that the microscopic characters of these kernels are like those of thc starch-bearing parent.

In none of these cases are the reciprocals reported as showing intermediate kernels. In one case (p. 67 and *pl. 1, f. 50*) he figures a kernel which is markedly pitted or wrinkled at one point while the rest of the kernel is smooth and flint-like. In another case (p. 56) a sweet corn by a sweet corn gave some kernels not so deeply wrinkled as the parents, though he states, "the chemical composition of the endosperm was not changed."

In two cases (pp. 70 and 76) he reports a sweet (*R. caerulaeodulcis*) pollinated on the one hand by a pop corn (*R. leucoceras*) and on the other by a flint (*R. vulgata*) as giving some kernels slightly dent-like in type in the F_1. The first of these cases he figures in *pl. 1, f. 72*, and the second in *pl. 1, f. 87* and in *pl. 2, f. 77*. In the latter case an entire ear is shown with most of the kernels slightly dimpled and a few with quite characteristic but poorly developed wrinkling. Correns also (p. 88) notes a tendency in crosses of sugar corn by flint types to what he regards as approaching a dent form of kernel in the F_1. He also notes (p. 89) that in crosses of flints by sweet types occasional kernels show an approach to the sweet type in the F_1. Correns found in his pure sweet race (*R. dulcis*) occasional kernels which are less wrinkled or almost smooth (pp. 39 and 40, *f. 4c*, *5b*, and *pl. 1, f. 22*) and explains them as having a larger air cavity and a larger mealy area making this a general explanation for intermediates (p. 39).

His figure of a section of such a kernel (p. 38) does not make clear that there is a larger air cavity in such grains but his figure (*pl. 1, f. 22*) gives a fairly good representation of the appearance of such

kernels as I have found them. Both these figures are from kernels of his pure race (*R. dulcis*). Correns does not give figures of any of his F_1 kernels, which he describes as "almost smooth," but apparently regards them as like those figured from the pure race. He describes the F_2 generations from only three of his sweet flint and pop crosses making the general statement that those described are typical of the whole series. In the first of these three, Exp. 107, (*R. rubra* × R. *dulcis*) × *R. dulcis* (back cross by recessive on F_1), out of 140 kernels he obtained 50 per cent wrinkled kernels, 5.8 per cent intermediate kernels, 44.3 per cent smooth kernels, the F_1 generation having given only smooth kernels.

The F_3 generation, Exp. 108, (*R. rubra* × *R. dulcis*) × *R. dulcis*, in which the wrinkled kernels of the F_2 were grown and pollinated by the original sugar parent (back cross on extracted recessive) gave three ears, two of which were all wrinkled, but in the third about one seventh of the kernels were "only slightly wrinkled." The parallel F_3 generation, Exp. 109, in which the smooth kernels of the F_2 were grown and pollinated by the original *R. dulcis* gave one large and two poor ears on one plant. Correns reports the kernels as "about half smooth and half wrinkled, some only slightly." He reports counting only part of the kernels, of which 82 were wrinkled and 2 almost smooth, 74 smooth; that is "53.2 per cent more or less wrinkled and 46.8 per cent smooth," the expectation being of course 50 per cent wrinkled and 50 per cent smooth.

Correns's Exp. 110 is identical with Exp. 108, so far as the characters sugar and starch are concerned. He considers this experiment open to question since of two plants, one gave three ears all wrinkled, the other gave one medium-sized and one small ear in which half the kernels were smooth and half were wrinkled "rather many only finely wrinkled or almost smooth" but otherwise the endosperm of typical sugar consistency. Whether or not these results are due to an error in records or manipulation there is no question that here again the intermediate sweet starch kernels appeared whatever their parentage may have been.

Exp. 111 again duplicates Exp. 109 so far as the characters sweet and flint are concerned. In the case of two individuals the proportions were 50.1 per cent smooth, 49.9 per cent wrinkled,

expectation 1:1, but from the third plant very many of the kernels were very slightly wrinkled though translucent like typical sweet kernels.

In the F_2 of his cross, *R. dulcis* sweet × *R. vulgata* flint, Exp. 112, in which four plants were allowed to pollinate freely among themselves, Correns reports that because of too late planting the ears for the most part did not become entirely ripe.

In Exp. 113, (*R. vulgata* flint × *R. caerulaeodulcis* sweet) × *R. dulcis*, which is a back cross of the recessive parent on the F_1 hybrid, he mentions that some kernels which were classified as sweet were almost smooth but their transparency indicated that they belonged with the sweet type. For Exps. 114, 115, 118, 119, 120, 121, 126, 127, no mention is made of kernels intermediate between sweet and flint.

SUMMARY OF CORRENS'S F_2 AND LATER GENERATIONS

107. 58 per cent of all kernels intermediate.
108. 1 ear of 3, one seventh of kernels only slightly wrinkled.
109. Some only slightly wrinkled.
110. Doubtful experiment, but in one ear rather many kernels only minutely wrinkled or almost smooth.
111. One plant of three gave many kernels, slightly wrinkled though translucent.
112. No intermediates mentioned.
113. Some kernels classed as sweet were almost smooth.

114, 115, 118, 119, 120, 121, 126, and 127. No mention is made of intermediates.
Fifteen experiments gave no intermediates.
Seven experiments gave intermediates.

The above summary of Correns's results on the F_2 and later generations from crosses between sugar and starch races shows that in seven out of fifteen experiments reported in which sweet kernels were expected some kernels of intermediate form appeared, in one case 5.8 per cent of the total number of kernels were intermediates. Correns in no way attempts to conceal this result but treats it as unimportant. He regards these kernels as sweet in type but with a larger air cavity and more mealy (p. 39). He seems not, however, to have selected these aberrant kernels and planted them, which of course, as he so frequently emphasizes, is the only proper test of the significance of such characteristics.

Correns in 1902 reports further on starch and sugar crosses. In an extensive test of the Mendelian formula he obtained 10,372

smooth kernels, 3,388 wrinkled kernels and 12 somewhat wrinkled. He includes the latter with the smooth instead of as above with the wrinkled, giving 75.4 per cent smooth, 24.6 per cent wrinkled. Again he does not report the behavior of the partly wrinkled kernels when grown. He also further tested the ratios obtained in a cross between Black Mexican sweet and Rice Pop Corn var. *leucoceras*, and found in the selfed F_2 generation an excess of smooth kernels. Instead of 75 per cent smooth and 25 per cent wrinkled he obtained in an extensive series 84.5 per cent smooth, 15.6 per cent wrinkled. In another extensive series 81.9 per cent smooth and 18 per cent wrinkled, no intermediates, are reported. Correns concludes these results are to be explained not on an assumption of segregation in some other than a 1:1 ratio but as due to partial failure of certain combinations to develop, or to selective or differential pairing. In the presence of a great excess of pollen on the silk certain grains might well take precedence by reason of their greater vigor in the particular combination possible to them. I am discussing these sweet × pop crosses in another paper.

As figured by Correns and as I find them, certain sharply pitted (*pl. 1, f. 50*) and chimaera-like (p. 39) kernels of the F_1 are quite different in appearance from the intermediately wrinkled kernels noted above. Correns does not test the behavior of these pitted and half and half kernels when grown and selfed. It is not impossible that they owe their appearance to special interactions of the germ plasms in the triple endosperm fusion and subsequent divisions and are not an index of what has happened in the fusion of the egg and male nuclei and the development of the embryo. I shall report elsewhere on the behavior of certain of these kernels when grown and selfed.

Correns, while making corn the type of his third class of the possible combinations of dominance and segregation (homodynamic schizogonic) in which the F_1 is more or less intermediate between the parents so that dominants, hybrids, and recessives are visibly different, does so on the grounds of the behavior of aleurone and endosperm colors, etc., and claims that the starch-sugar pair are heterodynamic with dominance of the starch character in the F_1 and later hybrids, (pp. 67, 86, 141).

East and Hayes ('11, pp. 33–34) had some four hundred hand

pollinated F_2's from crosses between sweet and flint, but report in detail on only one fourth of them, the remainder showing as they say "nothing different." They (p. 34) state that in the F_1 dominance is apparently complete. "In no case was there the slightest difference between the homozygous and the heterozygous seeds either in outward appearance or in the character of the starch cells when examined microscopically" though they note the occasional occurrence of the curious chimaera kernels with one side smooth, the other side wrinkled, which were also observed by Correns and others. They further concluded that the characters starchy and sweet are the same in all races so that all crosses behave alike. They had not of course tested at this time the crosses between waxy and sweet, later described by Collins.

East and Hayes report, however, that ears intermediate between sweet and flint do appear in various races of sweet corn and may give trouble to canneries since they transmit the character. They state that such ears appear in ratios not to exceed one in 10,000, but do not give the detailed statistical data on which the numbers are based. They also report one case in which three semi starch ears appeared in the progeny of an extracted recessive from a cross of Illinois High Protein Dent by Black Mexican Sweet. The entire ear was "rather uniformly semi starchy." The offspring of its more starchy kernels varied from as starchy as the parent to more starchy. Those from the less starchy kernels were in part good sweet kernels and in part semi starchy. Seeds could be selected which formed a series running from true sweet to true starchy. They reject the idea of impure segregation as accounting for such observations and hold that "dominant starchiness—if it is the same dominant starchiness—has been formed anew." They recognize also that certain races of sweet corn (Crosby) tend to have plumper kernels than others. Still in spite of all this they persist in regarding the factors for sweet and starchy as fixed and recognizably distinguishable categories. In a footnote (pp. 40–44) they argue the possibility that when pop corns are pollinated by sweet corns the smaller size of the kernels on intermediate ears may lead to their being more nearly filled by the endosperm materials and hence less wrinkled in appearance, they do not however give any further data on this

point from their own work. East and Hayes believe (p. 42) that these intermediates are not an evidence of the mixing of the sweet and starch characters but are due to progressive variations constantly taking place in small number along paths that have been passed before, and assert like Correns the dominance of the starch character over the sweet character, regarding the behavior of the two characters as an example of a simple Mendelian monohybrid.

I have reviewed the work of Correns and East in some detail on this point to show that from the first the ocurrence of such intermediates constituting exceptions to the simple formula for a Mendelian monohybrid were observed though they were regarded as unimportant from the theoretic standpoint. In spite of these observed cases of intermediates the combination of sweet with starch corns is made a standard type to illustrate Mendelian behavior in such summaries and general discussions as Correns's "Die neuen Vererbungs-Gesetze" ('12); Baur's "Einführung in die experimentelle Vererbungslehre," 2d edition ('14); Haecker's "Allgemeine Vererbungslehre" ('11); and even the new manual, "Genetics in Relation to Agriculture," by Babcock and Claussen ('18).

It is highly desirable, it seems to me, to know whether in attempting to maintain sweet races at their highest perfection and in breeding for new varieties it is necessary to exclude these intermediates in selecting seed. East and Hayes, as noted, make the general statement that as rather rare mutants they may cause considerable trouble to canners but without referring to specific instances.

Jones ('19) reports the continuance of a selection experiment with the three intermediate ears obtained by East and Hayes, and referred to above. The aim of the experiment was to recover, if possible, the parent starchy and sweet types by selecting from the selfed offspring of this intermediate. Beginning in 1907 the selection for starchy was carried through ten generations and that for sweet through nine generations. Jones obtained in this way a sweet race whose kernels still vary somewhat in the amount of opaque substance which they contain, though in general they are good sugar types and what he calls a pseudo-starchy race, in which the kernels are in some ears perfectly plump while in others there

may be areas on a few seeds which closely resemble the wrinkled condition of sweet seeds. In general it is stated this pseudo-starchy race when crossed with pure starchy races gives in the F_2 segregation into sugary and starchy kernels as if it had been a so-called pure sweet though the F_2 kernels so obtained show considerable tendency to pseudo-starchiness in later generations in a fashion that makes the results hard to classify. The explanation of his observations, Jones believes, is to be sought in the recognition that more factors are concerned in the determination of the sweet and starch pair of characters than had before been realized.

He makes no claim to have reached an adequate or theoretically satisfying analysis from the Mendelian standpoint. His assumed three factors are merely taken "as an illustration" and he speaks of the "indefinite nature of the character."

Jones refers (p. 388) to other cases he has observed in which intermediate kernels have appeared in starch and sugar corn crosses, though he expresses no opinion as to the frequency of their occurrence, and leaves the question of their nature and origin much as it was before. He recognizes the possible influence of the fact that the mother plant is always one generation in advance of the endosperm, though a real test of the significance of this situation is difficult to achieve.

On the assumption of relatively fixed unit factors, it is rather striking when this intermediate condition has appeared that new and definite combinations of the factors assumed are so difficult to achieve. Neither the pseudo starchy nor the segregated sweet, either in appearance or behavior, when bred seem quite to meet the standards of a homozygous race in the strict sense of Johannsen. We seem to have here the familiar phenomenon which was known to the older breeders as "breaking up" of types in the second and following generations as a result of hybridizing. From the standpoint of current theories we are inclined to focus our attention upon the possibility of recovering parent types after hybridizing while the older breeders regarded this phenomenon, though familiar, as of little interest compared with the cases in which "breaking up" occurred. The search was frequently so far as hybridization was used in breeding for practical ends for a cross in which breaking up would occur. A species with desirable basic

qualities of color, form, habit of growth, etc., was tested in various combinations until one was found which would give a series of variants of these basic qualities, such as we find in so many groups of cultivated plants.

It is to be hoped that Jones's experiments can be continued till an adequate unit factorial analysis for corn is, if possible, attained. The economic importance of the crop will certainly justify this procedure. Judging his data as they stand, however, it seems to me that the assumption of fluctuating variations and mutual modification of the germ plasms with each succeeding sexual reproductive cycle of synapsis, chromosome reduction, cell and nuclear fusion and chromosome pairing fits the facts much better than that of numerous fixed unit factors merely shifting their interrelations through the almost endless number of the mathematically possible combinations which, it is assumed again, they can enter with equal freedom.

My results agree with those of Jones that these intermediate kernels tend rather strongly to propagate their kind and that races with a strong tendency to their production can be isolated by selection. I am discussing elsewhere the possible importance of such races as what I have proposed to call meal corns. If corn is to be used increasingly as a food more attention should be paid by breeders to improving the flavor and general palatability of corns to be used in making meals.

In my own work intermediates have appeared in practically all of my crosses between sweets and flints, dents, flour corns, and pop corns. I have also observed cases of the spontaneous appearance of intermediate kernels in the pure bred Black Mexican Sweet and some other sugar corns which I have used. Such intermediate kernels in so-called pure races occur scatteringly on occasional ears and I have observed one ear which showed a general tendency to this condition. This ear probably came from an accidentally planted intermediate kernel. As noted above Correns does not report on any attempts to learn how the hybrid F_1 and F_2 kernels which he reports as "slightly wrinkled" or almost smooth would behave when grown and selfed or crossed back on their sweet or starch parents. The occurrence of such intermediates arising by all the various methods noted is of particular interest in view of the

tendency to overlook such fluctuating differences in the interest of attempts at broad generalizations.

I have endeavored to settle the points here involved and have grown a number of such intermediates which have appeared in various crosses between sweets, and flints, dents and pops.

The study of these endosperm characters is of special interest since the endosperm nuclei in general are the product of a triple nuclear fusion; in each case two nuclei from the mother combine with one from the male parent. The effect of this unequal representation of the two parents in the endosperm can be checked up by comparison with the expression of the same characters as transmitted to the next generation through the embryo which arises from the normally fertilized egg. The morphological nature and phylogenetic origin of the triple fusion in forming the primary endosperm nucleus have not been as yet worked out, but functionally and from the genetic standpoint it is a triploid growth which is crowded out and absorbed by the normal embryo. The study of reciprocal crosses with reference to the expression of these endosperm characters afford ideal conditions for determining the effects of a double as contrasted with a single set of chromosomes from the same parent, so-called dosage phenomena, etc. I shall not take up these questions in the present paper since I desire first to establish and clear up the facts as to the occurrence of intermediates between starch and sugar corns and the behavior of these intermediates when grown and selfed.

The interesting paper by Weatherwax ('19) establishes the fact that the embryo sac in corn is formed after the manner of the dicotyledonous rather than the lily type so that there is no possibility that either of the polar nuclei which fuse in the endosperm nucleus or their parents were formed by a reduction division and the possible complications as to the so-called genetic constitution of the nuclei of an endosperm of the lily type are not present in corn.

I have worked with the following races:

Four flints: Canadian Early Yellow, Longfellow, Long White Flint, and Hall's Golden Nugget.

Eight dent corns: Wisconsin White Dent, Silver King, Bloody Butcher, Gaunt's Golden Dent, Long's Champion Dent, King Philip Red Cob, Eureka Dent.

Six sugar corns: Crosby's Early, Country Gentleman, Ruby Sweet, Golden Bantam Sweet, Golden Cream Sweet, and Stowell's Evergreen.

Five flour corns: Red Squaw, Blue Flour (Pink Flour, Yellow Flour, and White Flour from Arikara Indians).

Six pop corns: Eight Rowed Pop, White Rice, Black Beauty Pop, Snowflake, Golden Tom Thumb, and California Golden.

With the exception of the corns from the Arikara Indians, these are all fairly common and well marked races which I have grown in selfed or inbred cultures parallel to my experiments with crossing and have found to come true to type except for such fluctuating variations as I am noting in connection with the experiments. That such fluctuating variations occur in both sexually and asexually reproduced series, is well established as noted, but that sexual reproduction favors their occurrence is, it seems to me, shown especially well by the results obtained in breeding corn.

My results can best be presented perhaps by reproducing life-size photographs of a series of ears (PLATES 1–3) illustrating the actual number, distribution, appearance, etc., of these intermediates from a characteristic generation in a series of experiments which I have carried on now for some six years. These figures can be regarded as typical of the fuller series reported statistically in the tables, which show the proportions of the various classes of kernels in the successive generations. They represent a stage in which the injurious effects of selfing are not yet seriously manifest. They are also illustrative of my results in all the sweet with flint or dent combinations noted below, with many of which I have worked for some six or seven years. I am reporting also on sweet with pop corn crosses and some further special cases in another paper.

PLATES 1–3, FIGS. 130 *a*–130 *f*, illustrate the F_3 of a cross between a large white dent obtained from Thorburn as Wisconsin White Dent, and the common Black Mexican sweet corn, also obtained from Thorburn. I am not reproducing figures of these two parent races since the types are well known and, though both ears are undersized and not well filled at the tip, due in part to selfing, FIG. 130 *a* for the sweet type and FIG. 130 *f* in its dent kernels for the starchy type may be taken as illustrating the kernel characters of the parents of the series. The kernels of Wisconsin

White Dent do not always show the pronouncedly wrinkled tip typically seen in dents. The kernels frequently show only a smooth transverse groove and the horny endosperm comes nearer the tip, leaving less of the opaque white endosperm. These kernels with less wrinkled tips have been called dimpled dents. They are well shown in the FIG. 130 *f* and as noted the dent kernels of this ear represent the dimpled dent kernels of the original starchy parent. They occur in the inbred ears but become much more numerous in the crosses with sweets. As in most dents the kernels at the butt and tip of the ear tend to pass over into the dimpled form or even to be quite smooth and flint-like, though generally showing more or less opaque endosperm.

I have not employed field tests on a large scale in my studies but have endeavored to use all the precautions for careful control in pollination with relatively small numbers of plants. I have used both the method of bagging the ears and tassels separately and transferring the pollen by hand, and the method of connecting tassel and ear by a paper tube and allowing the pollen to reach the silk directly. In spite of the fact that only one crop per year can be obtained, the large numbers of kernels on an ear, all produced under quite similar conditions, and the possibility of checking up results year after year on the preserved material in a fashion quite impossible with flower colors, etc., make corn a favorable material for such studies on the variation of characters, etc.

As noted above, there is general agreement as to the occurrence of intermediates between sugary and starchy kernels. I shall report particularly the numbers in which these intermediate kernels occur in the successive generations and their behavior when grown and selfed.

I have carried the cross between Wisconsin White Dent and Black Mexican Sweet, both obtained from Thorburn, through four generations, from 1912–1916 and will give my results with this series in some detail as noted, since they are illustrative of all my results in crossing sweet and flint or dent types. The tassels and ears were bagged separately for the most part though in some cases they were connected directly by paper tubes.

Three ears, 5 *a*, 5 *b*, and 5 *c*, were obtained in 1912 by pollinating the Wisconsin White Dent with pollen from the Black

Mexican Sweet and showed no intermediate kernels. They varied from a wrinkled to a dimpled or rather flint like dent, but showed no evidence of xenia so far as the starch sweet characters are concerned; the color inheritance I shall discuss elsewhere.

I obtained thirteen selfed ears of the F_2 generation (Nos. 129 *a–f*, six ears, and 130 *a–g*, seven ears) in 1913. In these ears the intermediate kernels when only superficially examined can be confused sometimes with the dents which also show wrinkling, though only at the tip. The translucency and general shrinkage of the sweet kernels when fully developed are however unmistakable, as are also the opaque white and shrunken tips of the dent. Some of the intermediates shade over into the sweet type and others toward the dent type. Those half way between sweet and dent can be recognized with certainty but others may be doubtful.

TABLE I. SELFED F_2 EARS OF CROSS WISCONSIN WHITE DENT × BLACK MEXICAN SWEET

Ear Nos.	Starchy	Intermediate	Sweet
129 *a*	277	5	96
" *b*	215	0	64
" *c*	315	3	119
" *d*	204	5	76
" *e*	329	5	133
" *f*	91	5	22
130 *a*	297	4	104
" *b*	154	4	43
" *c*	138	2	41
" *d*	239	13	63
" *f*	279	21	84
" *g*	345	6	124
	2,883	73	969

The classification of the kernels from these thirteen ears is given in TABLE I, which shows in the totals 2,883 starchy kernels to 969 sweet kernels, and 73 apparently intermediate kernels. This is a ratio of about 73.45 per cent starchy: 1.85 per cent intermediate: 24.68 per cent sweet. If we class the intermediates with the starchy kernels we have a ratio per four of 3.01 starchy: .98 sweet. If we divide the intermediates equally between the starchy and the sweet kernels we have a ratio per four of 2.97 starchy: 1.02 sweet. If we class the intermediates with the sweets,

as Correns has done we have a ratio per four of 2.93 starchy: 1.06 sweet. The divergence from the Mendelian ratio is least when the intermediates are classed with the starchy kernels though the basis of their selection was that they were somewhat wrinkled. As noted above we can also distinguish here an intermediate in the starchy kernels between dent and flint. In these so-called dimpled dent kernels the opaque whiteness and large wrinkled depression of the tip of the dent kernel is much reduced. They shade over into typical dents on the one hand and typical flints on the other, and the classification is not always easy to make. I have not attempted to separate them here but have done so in connection with the ears photographed from later generations.

Kernels from four of these F_2 ears, 129 *a*, 129 *c*, 130 *a*, and 130*d*, were grown and selfed in the next (F_3) generation (1914). The kernels were selected with reference both to the inheritance of the sweet and starchy characters and the aleurone color. I shall consider here only the results with the sweet and starchy characters leaving the data as to the inheritance of aleurone color for a later report. I will take up first the results obtained from selected intermediate kernels.

Ear 130 *d*, showing a fair number of intermediate kernels, was selected as the parent for the next generation of intermediates. The thirteen white intermediate kernels were planted and six ears were obtained from this lot in 1914, which ranged from one (164 *a*) which had almost all its kernels typical sweets to another (164 *f*) which had a large proportion of dimpled dent and more typical dent kernels, though the photograph is hardly adequate to distinguish the latter from the dimpled type, especially in the rows in which the kernels are seen directly in end view. I have taken this F_3 series as illustrating as fully as possible the facts regarding these intermediates and have had them photographed and reproduced life size so that the degree and character of the fluctuations can be studied as they appear in the originals. This seemed preferable to giving a larger number of less perfect illustrations. The series is shown in the photographs and the classification of the kernels is given in TABLE II, section 1, *A*. A dark intermediate kernel from the same ear (130 *d*) gave an ear of all sweet kernels (167 *a*) like 164 *a* of the white series and is included

in the table though not figured, as it shows nothing further than is shown by 164 *a*.

TABLE II. CROSS WISCONSIN WHITE DENT × BLACK MEXICAN SWEET

1. F_3 EARS FROM SELFED F_2 EAR 130 *d*, 1914

A. Selected intermediate kernels planted

Ear Nos.	Dent	Dimpled Dent	Flint	Interm.	Sweet
164 *a*.....	0	0	0	8	163
" *b*.....	0	0	0	133	71
" *c*.....	0	3	0	132	52
" *d*.....	0	0	0	123	62
" *e*.....	0	12	0	177	56
" *f*.....	32	86	40	43	35
167 *a*.....	0	0	0	0	309
	32	101	40	616	748

The pure starchy kernels as noted vary from flints which are quite smooth and more or less translucent and horny to dimpled dents in which there is a slight groove at the tip. From this dimpled dent form they range further toward more typical dents with wrinkled as well as grooved tips and with a well marked opaque white color due to intercellular air spaces.

Ear 167*a* is a pure sweet showing no marked intermediates, as noted; ear 164*a* is almost pure sweet, showing eight intermediate to 163 sweet kernels, a ratio of about 4 per cent intermediates to 95 per cent sweet. The intermediates here also incline toward the sweet type in amount of wrinkling and translucency, though easily distinguishable from the typical sweet kernels.

As the photograph shows, ear 164 *f*, also from an intermediate kernel is in general quite of the dimpled type, but with conspicuous sweet and intermediate kernels scattered among the dent-like kernels. The classes here are 158 starchy to 43 intermediate and 35 sweet. If we divide the intermediates equally between the starchy and the sweet classes, we shall have 179.5 starchy to 56.5 sweet, or 3.042 starchy to .957 sweet, a good Mendelian hybrid ratio. But if as Correns did, we add the intermediates to the sweet class, we get 2.67 starchy to 1.32 sweets. The extremes of the six ears range then from one almost pure recessive ear to one more like a so-called hybrid ear as they have been perhaps sometimes classed. It is not impossible that if larger numbers had

been planted, an ear approximating a pure dominant would have been obtained. The results become clearer from a consideration of the remaining four ears from these intermediate kernels. It is obvious at once, however, that the range of variation in the characters sweet and starch in these F_3 intermediate kernels extends in some cases at least so as to include both of the original parent types. There is no evidence in this case of the segregation at once of a factor or group of factors for intermediate nor of the production of a mutant which then at once breeds true.

The other four ears of the series, ears 164 *b*, *c*, *d*, and *e*, bring out still more clearly the fluctuating character of the qualities here involved. Ear 164 *b* gives only sweet and intermediate kernels, 133 intermediate to 71 sweet, a ratio of 34 per cent sweet to 65 per cent intermediate. The translucency of most of the kernels gives the ear the general appearance of the sweet type but the opaque white of the intermediate kernels is also conspicuous and their less wrinkled surfaces make them easily recognizable in the photograph.

Ear 164 *c* shows three dimpled dent kernels with 132 intermediate and 52 sweet, a ratio of about 1+ per cent starchy: 70+ per cent intermediate: 27+ per cent sweet. The number of intermediates is larger here again than the number of sweet kernels, and three dimpled kernels appear.

Ear 164 *d* should probably be classed as giving only sweet and intermediate kernels though it is difficult to be certain of the character of the kernels at the ends of two of the rows and two kernels should perhaps be classed as flints. Counting them as intermediates we have 123 intermediates to 62 sweets, something like a ratio of 2:1. The position of this ear in such a series as we have here is perhaps doubtful. It has a larger proportion of fully wrinkled kernels than ear 164 *c*, but on the other hand its intermediates tend more toward the dent type, especially in color. The ear in general shows more opaque white than ear 164 *c*, in which the translucency due to the sweet character is more in evidence.

Ear 164 *e* gives 12 dimpled dent kernels, some of which are almost flint-like; 177 intermediate and 56 sweet, a ratio of 4+ per cent starchy: 72+ per cent intermediate: 22 per cent sweet.

The proportion of pure sweets to intermediates is somewhat reduced. If we here class the intermediates with the starchy kernels we should have a ratio per four of 3.08 starchy and intermediates to .91 sweet.

The translucency of the intermediates is much less in this ear than in ear 164 *c*. The kernels tend also to be less wrinkled and as the photograph shows the ear has a greater resemblance to the parental dent type than the figures in the table indicate.

These four ears 164 *b*, *c*, *d*, and *e*, show in general two intermediates to one sweet kernel and it would be quite possible to conceive of a Mendelian factorial hypothesis to fit their case. Taking the whole series the facts suggest rather that in selecting intermediates one is inclined to select kernels of pronouncedly intermediate character and pass by those which are doubtful, leaving them in the sweet and starchy classes. Allowing for this tendency in selecting there would none the less seem to be evidence that intermediates tend rather to vary toward the sweet character than toward the starchy character. All six ears show large proportions of typical sweet kernels while only three of them show typical starchy kernels.

It is obvious that there is a marked tendency to the perpetuation of the intermediate condition when once it has appeared. Still it can by no means be maintained that intermediate kernels at once breed true. As shown in the table two ears (164 *a* and 167 *a*) from kernels selected as intermediates appear to be almost typically sweet, and one ear (164 *f*) has a high percentage of typically starchy kernels; 66+ per cent of starchy kernels, 18+ per cent of intermediates and 14+ per cent of typical sweet kernels. The remaining four ears vary in their proportions of intermediate kernels, to sweet kernels, neglecting the starchy kernels, from, roughly, 2:1 to 3:1.

This fluctuation in the occurrence of intermediates is still further illustrated in the offspring of six further lots of kernels selected from this same F_2 ear (130 *d*) to test the behavior of what appear to be pure sweet and pure starchy kernels, respectively. These lots were selected with reference to endosperm color as well but we shall consider only the sweet starch characters here. Four of the lots (Nos. 160–163 inclusive) were typical dimpled

dents and two lots consisted of typical sweet kernels (Nos. 165, 166). The dimpled dent lots were selected to represent colors from dark or blackish to white but we may treat them as one series with reference to the starch sweet characters. Twenty-four ears and nubbins were obtained from these dimpled dent starchy kernels (Nos. 160–163) of which twelve showed few intermediates and almost all dent, dimpled dent, and flint like kernels (extracted dominants) and twelve showed conspicuously dent, dimpled dent, flint, intermediate, and sweet kernels (F_3 hybrids).

TABLE II (*con.*)

B. Selected dimpled dent kernels planted

a. Mixed ears (hybrids) obtained

Ear Nos.	Starchy.	Intermediate.	Sweet.
160 *b*–1	147	35	13
" *b*–2	183	26	17
" *d*	17		9
" *f*	27	10	3
" *g*	129	14	37
" *h*–1	159		56
" *h*–2	33	3	58
161 *a*	126	13	47
162 *a*	89	5	34
" *b*	142		43
" *m*	179	43	1
163 *d*	159	5	51
	1,390	154	369

The proportion of intermediates in all these ears as will be seen is much smaller than in the case of the offspring of the F_2 kernels selected as intermediates. The ears of this class of F_3 hybrids as shown in TABLE II, section 1, *B*, *a*, give 1390 starchy to 154 intermediates to 369 sweet kernels, that is 2.9 starchy to .32 intermediate to .76 sweet. There are here in addition to the kernels which are plainly intermediate some others which approximate starchy kernels on the one hand and sweet kernels on the other. The classification is difficult in some cases since there is really a series from starchy to sweet. I have put in the class of intermediates only those that were plainly from their form and degree of translucency neither typical starchy nor typical sweet kernels. Here as in other cases it would be possible to make more than one class of intermediates but the lines of distinction would

be vague. If we should make but two classes putting all kernels that show any trace of wrinkling together we should have 1,390 starchy kernels to 523 more or less wrinkled and translucent kernels, a proportion per four kernels of 2.90 : 1.09. If we should divide the intermediate group equally between the starchy and sweet classes we should have more nearly an exact Mendelian ratio, 1,467 starchy to 446 sweet, that is 3.06 starchy to .93 sweet, as noted. Correns as noted treated the "slightly wrinkled" and "almost smooth" kernels he observed as sweet kernels.

The twelve ears which showed no typical sweet kernels gave a very low proportion of intermediates. Seven of these ears give no intermediates. The other five ears give only from one to four intermediate kernels, the total being 2,397 starchy to 11 intermediate kernels, 267 starchy to 1 intermediate. The classification is difficult here also and I have included only kernels of undoubtedly intermediate appearance in that class. The numbers of kernels of the different classes for these ears are given in TABLE II, section 1, *B*, *b*. As noted they are the so-called extracted dominants.

TABLE II (*con.*)

b. Slightly mixed ears (dominants) obtained

Ear Nos.	Starchy	Intermediate	Sweet
160 *a*	236		
161 *b*	182		
" *d*	196		
163 *a*	319		
163 *b*	194	4	
" *c*	267	1	
" *e*	74		
161 *c*	297	3	
161 *e*	202	2	
160 *c*	114	1	
160 *e*	173		
160 *i*	143		
	2,397	11	

From the two F_2 lots Nos. 165 and 166 of extracted sweet kernels which came from ear 130 *d* nine F_3 ears and nubbins were obtained (165 *a–d* and 166 *a–e*). The parent kernels and the ears obtained differ in aleurone color but as in the previous case of dents and flints, they may be considered as one series with reference to the characters sweet and starch. Of these nine ears seven

were relatively good sweets with only a small number (two to eight) of intermediate kernels while two (Nos. 166 *a*, *c*) showed a larger number of intermediates, one of them (166 *c*) showing also four kernels that I have classed as dimpled dents and thirteen kernels that I have classed as flints. This ear also showed six kernels in the special class of intermediates which are chimaera-like, with one half plump starchy and the other half wrinkled sugary in appearance. This is the highest number of such kernels that I have so far observed in a single ear. I have classed them with the intermediates in my general averages but their number is too small to appreciably affect the results.

TABLE II (*con.*)

C. Selected sweet kernels planted

c. Mixed ears, but prevailingly sweet (recessives)

Ear Nos.	Dimp. Dent	Flint	Intermediate	Sweet	Chimaera
166 *a*.....			61	255	
166 *b*.....			7	218	
166 *c*.....	4	13	56	70	6
166 *d*.....			3	337	
166 *e*.....			3	50	
165 *a*.....				225	
165 *b*.....			8	197	
165 *c*.....			2	117	
165 *d*.....				25	
	4	13	140	1,494	6

The classes and numbers of kernels for these nine ears (165 *a–d*, 166*a–e*) are given in TABLE II, section 1, *C*, *c*, and show when compared with the results given in TABLE II, section 1, *A*, that in this case the number of intermediate kernels found in ears from F_2 kernels selected as sweet is much smaller (about 8 per cent) than in ears from kernels selected as intermediate (about 40 per cent. In ears from starchy kernels there is only about 3 per cent of intermediate kernels (TABLE II, section 1, *D*).

We have clearly enough, it seems to me, in the offspring of this single F_2 ear (130 *d*) the picture of a case of fluctuating modification of characters by crossing with a further fluctuating tendency to inheritance of the modification suggesting the possibility of obtaining a fairly pure race intermediate, in respect to the characters considered, between the parent races.

The data furnished by the offspring from the further ears of the same F_2 generation (130 *a*, 129 *a*, *c*) suggest the same conclusion. These lots again were selected with reference to variations in aleurone color and for this reason further intermediates were not planted, but as before we shall consider at this time only the starchy and sweet characters.

TABLE II (*con.*)

D. Relative proportion of intermediate kernels obtained in F_3 from Wisconsin White Dent × Black Mexican by planting intermediate, as compared with starch and sugar kernels from ear 130 d

		From starchy kernels, 34 ears		From intermediate kernels, 7 ears	
		Typical	Interm.	Typical	Interm.
Extr. hybr. 12 ears	starchy	1,390		173	616
	sweet	369	154	748	
Extr. dom. 12 ears	starchy	2,397	11		
	sweet				
		4,156	165		
		From sugar kernels			
Extr. rec. 9 ears	starchy	17			
	sweet	1,494	146		
		1,511	146	921	616

From ear 130 *a*, I grew in 1914 plants from four types of kernels, Nos. 155–158, 155 from colored flint kernels, 156 from white flint kernels, 157 from colored sweet kernels, 158 from white sweet kernels. From the starchy kernels eighteen ears were obtained. Ten of these ears would be classed as hybrids and in addition to typical starchy and sweet kernels, gave a much higher proportion of intermediates than the eight ears which would be classed as extracted dominants. In the former, TABLE II, section 2, *A*, *a*, there is one intermediate to thirty-nine starchy and sweet, in the latter, TABLE II, section 2, *A*, *b*, only one intermediate to 138 starchy. If we divide the intermediate kernels from the ten hybrid ears from this parent equally between the starchy and sweet classes we get 1772.5 starchy to 524.5 sweet, a ratio per four of 3.084: .913.

From the extracted sweet kernels (Nos. 157 and 158) ten ears were obtained. Eight of them were quite true to type as sweets

but one (158 *b*) showed a high percentage of intermediates and one a considerable percentage that were not fully wrinkled (157 *d*).

TABLE II (*con.*)

2. EARS FROM SELFED F_2 EAR 130 *a*

A. Starchy kernels planted

a. Mixed (hybrid) ears

Ear Nos.	Starchy	Intermediate	Sweet
155 *a*	82		15
" *g*	116		39
" *j*	242	7	78
" *h*	240	5	55
" *l*	207	17	45
156 *a*	145	10	33
" *b*	214	3	65
" *c*	222	1	82
" *d*	144	12	36
155 *e*–1	132	2	48
	1,744	57	496

b. Slightly mixed ears (extracted dominants)

155 *b*–1	96	1	
" *d*	329	1	
" *f*	240	10	
" *h*	141		
" *i*	434		
" *m*	140		
156 *e*	160		
" *f*	118		
	1,658	12	

TABLE II, section 2, *B*, *c*, gives the composition of these ears in detail and shows that from kernels selected as typically of the wrinkled sweet type when selfed one in every thirteen of the offspring appeared as intermediates, or as less wrinkled than is characteristic. This is a higher proportion of intermediates than was obtained from the so-called hybrids from the same parent ear (130 *a*) which gave one intermediate to thirty-nine starchy and sweet, and a very much higher proportion than came from the corresponding extracted dominants which gave only one intermediate to 138 starchy. The five full starchy kernels in ear 158 *a* and the four similar kernels in ear 157 *i*, were possibly from stray pollen though several of the intermediate kernels on ear 158 *a* which were probably the result of selfing were very close to starchy types while showing undoubted wrinkling.

TABLE II (*con.*)

B. Sweet kernels planted

c. Slightly mixed ears (recessives)

Ear Nos.	Starchy	Intermediate	Sweet
158 *a*	5	10	316
" *b*		78	103
" *c*		4	139
157 *c*			386
" *d*		32	171
" *e*			249
" *f*		23	105
" *g*			325
" *h*		11	128
" *i*	4	2	242
	9	160	2,164

From ear 129 *a* of this same cross, Wisconsin White Dent × Black Mexican sweet, eight different lots of kernels (Nos. 168–175) were planted in 1914. Lots 168, 169, 170, and 175 were from kernels dimpled dent in type. Lots 171–174 were from sweet kernels. No. 173, which was a pale sweet kernel, failed to produce any ears.

From the dimpled dent kernels 168, 169, 170, and 175 I obtained twenty ears. Six ears consisted largely of pure starchy kernels with few intermediates. These would be classed as extracted dominants. The number of starchy kernels and the number of intermediate kernels for each of these ears is given in TABLE II, section 3, *A*, *a*. The proportion of intermediates to starchy kernels for the six ears is about 1:185.

Sixteen ears gave both starchy and sweet kernels and would be classed as hybrids. The number of starchy intermediate and sweet kernels for each of these ears is given in TABLE II, section 3, *A*, *b*. For the whole series of sixteen ears there is a proportion of one intermediate to ninety sweet and starchy taken together. If we divide the intermediates, putting half of them with the starchy and half with the sweet kernels, we have 1981.5 starchy to 660.5 sweet kernels an exact 3:1 ratio. Assuming that the differences in wrinkling and translucency are really negligible and that some of the intermediates really belong with each of the two starchy sweet classes, such results as these and the preceding have been generally regarded as evidence of so-called purity of stock, homozygosity.

TABLE II (*con.*)

3. EARS FROM SELFED F_3 EAR 129*a*

A. Starchy kernels planted

a. Slightly mixed ears (dominants)

Ear Nos.	Starchy	Intermediate	Sweet
168 *a*	146	2	
" *m*	149	1	
169 *a*	232	2	
" *d*	92		
170 *b*	202		
" *d*	99		
	920	5	

b. Mixed ears obtained (hybrids)

168 *b*	199	5	94
" *c*	79	3	26
" *d*	178	7	45
" *e*	94		27
169 *b*	188	1	40
" *c*	89		24
" *e*	73		12
170 *a*	208		64
" *c*	133		59
" *e*	184		52
" *f*	93		31
" *g*	59	1	16
" *h*	89		47
" *i*	85		27
175 *a*	160	10	60
" *b*	56	2	22
	1,967	29	646

B. Sweet kernels planted

c. Slightly mixed ears obtained

171 *b*			176
" *a*			218
" *c*		9	138
" *m*			191
172 *a*		3	171
" *b*			77
" *c*			29
172 *d*			51
174 *a*			84
" *c*	3		90
" *d*			91
" *b*			120
	3	12	1436

From the kernels of this F_2 ear (129 *a*) selected to represent the sweet type I obtained twelve ears, nine of which showed only sweet kernels. Two (171 *c* and 172 *a*) showed respectively nine and three intermediate kernels. One ear (174 *c*) showed three full starchy kernels which may have been due to stray pollen as there were no intermediates on this ear. The classes of kernels for each of these ears is given in TABLE II, section 3, *B*, *c*.

From ear 129 *c* of the same cross four lots were planted, two (Nos. 176 and 178) consisting of dimpled dent kernels and two (Nos. 177 and 179) consisting of sweet kernels.

TABLE II (*con.*)

4. EARS FROM SELFED F_3 EAR 129 *c*

A. Starchy kernels planted

a. Mixed ears obtained (hybrids)

Ear Nos.	Starchy	Intermediate	Sweet	Chimaera and pitted
176 *a*	84	7	38	
" *c*	118	11	32	
" *d*	152		49	
" *e*	137	3	34	
" *f*	96	13	8	
" *m*	130	4	55	
178 *a*	293		88	5
" *c*	172	18	27	1
" *d*	191	1	86	
" *e*	163	1	61	
" *f*	105	6	37	
	1,641	64	515	6

From the dimpled dent kernels, thirteen selfed ears were obtained, two with for the most part pure starchy kernels which would be classed as extracted dominants and twelve giving starchy, intermediate, and sweet kernels which would be classed as extracted hybrids. In TABLE II, section 4, *A*, *a*, the composition of the mixed ears (extracted hybrids) is shown. The six kernels which show pitting, or one half sweet and one half starch (chimaera kernels) are counted with the intermediates. If the intermediate kernels are divided equally between the starchy and sweet classes we have here again an almost perfect Mendelian ratio, 3.008 starchy: .990 sweet. There is one intermediate kernel to thirty starchy and sweet kernels, a larger proportion than is found in the starchy ears.

The composition of the two extracted dominant ears is shown in TABLE II, section 4, *A*, *b*. The proportion of intermediate to starchy kernels is about 1:50.

TABLE II (*con.*)

b. Slightly mixed ears obtained (dominants)

Ear Nos.	Starchy	Intermediate	Sweet
176 *b*.....	163	5	
178 *b*.....	243	3	
	406	8	

From the sweet kernels, Nos. 177 and 179, seven ears were obtained whose composition is shown in TABLE II, section 4, *B*, *c*. Four of these ears show only sweet kernels while the other three show from one to fourteen intermediate kernels, the ratio for the whole group being about one intermediate to fifty-seven sweet kernels.

TABLE II (*con.*)

B. Sweet kernels planted

c. Slightly mixed ears obtained

Ear Nos.	Starchy	Intermediate	Sweet
177 *a*.....		1	322
177 *b*.....			238
177 *d*.....			216
177 *e*.....			28
177 *f*.....			32
179 *a*.....		14	193
179 *b*.....		6	182
		21	1,211

In 1915 this Wisconsin White Dent and Black Mexican Sweet cross was grown only for endosperm color in the attempt to isolate a pure blue race, and no intermediates between sweet and starch were planted, as the starchy kernels show the color more easily, especially in variegated kernels.

The fourth generation of these intermediates from the cross of Black Mexican Sweet by Wisconsin White Dent was grown in 1916. In this year an out cross was made in order to test the behavior of the intermediate condition in combinations from different sources. A series of kernels from one of the above F_3

selfed ears was grown and the silks pollinated from another coffee-colored intermediate obtained by crossing two well-marked sweet races. The male parent of this intermediate was the Black Mexican Sweet used in the parentage of the series so far considered. The female parent was Ruby Sweet, a form obtained from Childs in 1913 and grown and selfed in that year. Kernels from one of these selfed ears were grown in 1914 and crossed with Black Mexican Sweet. The F_1 ears so obtained showed a mixture of sweets and intermediates and the intermediate kernels selected from one of these ears (74 *a*) were made the starting point for a series of intermediates which have been continued now through four inbred generations (1914–1918). These intermediates did not at once breed true. They showed varying proportions of sweets, intermediates, and fully smooth, flint-like kernels. Halstead ('07, '08, '09) has described a similar case of the origin of an intermediate Malamo from two sweet races, Malakan and Premo. He bred the type for a number of years with open pollination and by selection of sweet and flinty kernels obtained a marked increase in the starchiness and sweetness respectively of the ears.

His test plots showed ('08) that "ears from the plot planted with flinty kernels were largely flinty while the sweet grains gave ears that showed as a rule very little tendency to produce starch." He did not obtain, however, in either case types which would breed true. They probably showed a wider range of variability than was represented in the parents.

I shall describe this series more fully in the discussion of the use of these intermediates between starch and sugar types as special meal corns. Intermediate kernels from an ear of the F_1 (74 *a*) of this Ruby Sweet × Black Mexican cross were planted and used as the male parent for a series of other intermediate types, including those between Wisconsin White Dent and Black Mexican Sweet which we have been considering. The male and the mother plants were planted in alternate rows and the mother plants were simply detasseled and left to open pollination from the coffee colored intermediate.

Three lots of kernels from ear 164 *b* (Table III, section 1, *A*) were planted in the 1916 plot as the F_4 generation of the Wisconsin White Dent × Black Mexican Sweet series. No. 750 consisted of

dimpled dent kernels, No. 751 of intermediate kernels and No. 752 of sweet kernels. All these were grown and pollinated by the intermediate from Ruby Sweet × Black Mexican, No. 763, as male parent. The ears obtained in this way were all small as a result of the selfing in the F_2 and F_3. The kernels selected as dimpled dents, No. 750, failed to come so no results in this particular combination were obtained.

The intermediate kernels from this ear gave two ears, 751 *a* and *d*, with almost wholly intermediate and sweet kernels, two ears on one stalk, 751 *c* 1 and *c* 2 wholly flint in type, and one ear, 751 *b* which gave flint, intermediate, and sweet kernels. The classes are shown in TABLE III, section 1, *A*; 48+ per cent are starchy, 31+ per cent intermediate, and 20+ per cent sweet.

TABLE III. OUT CROSS IN 1916, F_3 OF RACE SELECTED AS INTERMEDIATES FROM WISCONSIN WHITE DENT BY BLACK MEXICAN SWEET × THE F_1 INTERMEDIATE FROM A CROSS BETWEEN TWO SWEET TYPES, RUBY SWEET × BLACK MEXICAN SWEET

1. EAR 164 *b* AS PARENT

A. Intermediate kernels planted

Ear Nos.	Flint	Intermediate	Sweet
751 *a*.....		186	77
751 *b*.....	114	67	67
751 *c*–1.....	78		
751 *c*–2.....	292		
751 *d*.....	3	61	57
	487	314	201

The distinction between sweet and intermediate in all these ears was very difficult in many kernels, though that there were the three classes present was obvious. The results are of interest as showing that in this out cross, though the new male parent came from two sweet parents, the capacity to produce kernels and even entire ears of the full starchy type has not disappeared in this intermediate series. The fully wrinkled sugar kernels are perhaps even more persistent though pure sweet ears were not obtained.

Three other nubbins, 754 *a*–*c*, from intermediate kernels of ear 164 *b*, were obtained from ears grown in the greenhouse but were too poorly developed to be considered.

The kernels selected as fully wrinkled, No. 752, from this F_3 ear (164 *b*) also gave a mixed result when pollinated by the Ruby Sweet × Black Mexican Intermediate. Four ears were obtained Nos. 752 *a* 1 and *a* 2 from the same stalk, 752 *b*, and 752 *c*. The classes of kernels are given in TABLE III, section 1, *B*. There are 42 per cent intermediate and 57 per cent sweet.

TABLE III (*con.*)

B. Fully wrinkled sweet kernels planted

Ear Nos.	Flint	Intermediate	Sweet
752 *a*–1		22	140
752 *a*–2		75	97
752 *b*		233	79
752 *c*		17	162
		347	478

The ears verge strongly toward pure intermediates in their general appearance but it is difficult if not impossible in the case of many kernels to decide whether they should be classed as sweet or intermediate. It seems quite unnecessary to figure these ears or the remaining ones of the series as the grades of wrinkling are similar to those shown in the figures given for the F_3 generation. A lot of intermediate kernels from ear 164 *c* showed the result of the selfing in the F_3 still more markedly. Fourteen small ears and nubbins were obtained all but two, 753 *c* and 753 *k*, were poorly filled. Ear 753 *c* was quite uniformly intermediate. Ear 753 *k* verged more toward sweet. The scattered kernels on the other ears and nubbins were hard to classify owing to the flattened and abnormal forms regularly found in such scattered kernels and I have not attempted to summarize the results of this planting.

A lot of intermediate kernels from the F_3 ear 164 *d*, sister to 164 *b* and 164 *c*, gave four ears, 754 *e*–*h*, with a large proportion of rather typically intermediate kernels. The classes are given in TABLE III, section 2. There are 55+ per cent intermediate, and 44+ per cent sweet. One ear, 754 *f*, showed more sweet than intermediate kernels. All four ears showed some kernels strongly verging toward flints in their appearance. These kernels are somewhat opaque and their wrinkling is very delicate, scarcely perceptible in some cases.

TABLE III (*con.*)

2. EAR 164 *d* AS PARENT (SEE TABLE II, SECTION 1, *A*)

A. Intermediate kernels planted

Ear Nos.	Flint	Intermediate	Sweet
754 *e*		65	53 Many flint-like
" *f*		102	146
" *g*		83	26 Many flint-like but minutely
" *h*		153	92 wrinkled kernels
		403	317

Ten small ears and nubbins, Nos. 758 *a–f* were obtained from the F_3 ear 164 *f*. The classes of kernels are given in TABLE III, section 3. There are a few scattering kernels in this lot which are plump and opaque and may be classed as starchy. The intermediates are for the most part quite typical. In the whole series there is a preponderance of sweet kernels but many kernels classed as sweets verge strongly toward intermediates. The ratios are .2+ per cent starchy: 46+ per cent intermediate: 53+ per cent sweet.

TABLE III (*con.*)

3. EAR 164 *f* AS PARENT

Intermediate kernels planted

Ear Nos.	Starchy	Intermediate	Sweet
758 *a*–1		127	54
" *a*–2		100	24
" *b*–1	1	106	48
" *b*–2		72	68
" *c*–1		44	69
" *c*–2		15	31
" *c*–3	1	82	84
" *d*	2	22	160
" *e*		20	180
" *f*		78	68
	4	666	786

Four small ears, Nos. 759 *a–d* were obtained from intermediate kernels from ear 166 *a*. The classes from these ears are given in TABLE III, section 4.

One ear, 759 *a*, is almost wholly sweet in type. The other three are markedly intermediate in general appearance, but many of the kernels are very hard to classify. The proportions are 55+ per cent intermediates and 44+ per cent sweet.

Considering this whole F_4 out cross generation, we find that when intermediate kernels were planted they predominate slightly over the sweet. The proportions are from intermediates: starchy 12+ per cent, intermediate 46+ per cent, sweet 41+ per cent. The appearance of the large number of flint kernels in the progeny of the intermediate kernels from ear 164 *b* is notable as showing

TABLE III (*con.*)

4. EAR 166 *a* AS PARENT

Intermediate kernels planted

Ear Nos.	Starchy	Intermediate	Sweet
759 *a*		4	259
" *b*		119	72
" *c*		198	22
" *d*		161	34
		482	387

the persistence of the capacity to return to a fully starchy type, especially since as noted the new male parent came as a cross from the two sweet races Ruby Sweet and Black Mexican Sweet. The sweet kernels planted from this same ear also gave a preponderance of sweet, 57+ per cent sweet to 42+ per cent intermediate.

GENERAL DISCUSSION

1. SIGNIFICANCE OF THE INTERMEDIATES

From these four generations of a cross between a sweet and a dent corn, the evidence is very clear, it seems to me, that what can be interpreted as a separation of the parental germ plasms in the reduction divisions and recombinations of the gametes so produced according to the laws of chance actually occurs as East and Correns found and as has been shown cytologically and assumed generally in Mendelian conceptions. It is, however, equally plain that provision must be made in such theoretic conceptions for the occurrence of intermediates. There is evidence of segregation (chromosome reduction) but not of the so-called purity of the gametes. We might assume here in accord with current practice factors acting as modifiers, inhibitors, etc., with varying efficiencies in the case of different kernels, but there is no adequate

evidence that any such assumed factors are distributed in the reduction divisions in any clear-cut and obvious fashion, such as the simple mono-hybrid ratios, and to name in the germ plasm the same qualities observed in the soma explains nothing and is merely the old preformationism in a modern guise.

Correns ('01) and East and Hayes ('11) have based their generalization that the qualities starchy and sugary make a typical Mendelian pair of characters in their segregation and recombination behavior on the assumption that intermediates behave, when grown and selfed, practically like the visibly more typical starchy or sweet kernels, except in rare cases of mutation, when as East reports an occasional intermediate ear (1 in 10,000) appears with no evidence that it is a result of hybridization and whose offspring tend to breed true, thus causing trouble to growers of sweet corn for canneries in case such ears are not avoided as seed.

That however both in their behavior in the following generation and in their appearance there is adequate ground for treating the intermediates as a special class is, it seems to me, sufficiently evident from the data given above. In TABLE II, section *1*, *D*, I have brought together and compared the results obtained by planting intermediates with those obtained by planting typical starchy and sugary kernels from ear 130 *d*. About 40 per cent of intermediates were obtained from planting intermediates, while ears from sweet and starchy kernels gave only about 5 per cent of intermediate kernels. The evidence from Correns's work as well as my own is overwhelming that such intermediate kernels do occur sporadically but quite commonly as a result of crossing as well as congenitally as a result of sexual reproduction in so-called pure races and that in whatever way they arise, they do not at once breed true. By selection the percentage of such kernels may be increased with fair probability in every case that rather pure races of intermediates may be established. Selection of intermediates through the F_2 and F_3 generations selfed followed by an out cross with an intermediate of different parentage gave as the progeny of one ear (166 *a*) three out of four ears with a considerable excess of intermediates and with no pure starchy kernels. The fourth ear was an almost pure sweet. The off-

spring of the other F_3 ears gave more mixed results. Since but one generation can be grown in a year, it is a slow process to test out the effects of selection, particularly in view of the bad effects of inbreeding, but it seems to me the results given are conclusive for this particular case at least, though the particular point with which I am concerned is to show that sporadically occurring intermediates arising in crossed ears do not behave when grown and selfed like ordinary sweet or starchy kernels, but show that the intermediate condition is also heritable in a very considerable degree.

There is evidence also that in the whole F_2 and F_3 of this cross of Wisconsin White Dent by Black Mexican Sweet, we not only obtain more intermediate kernels by planting intermediates than are obtained by planting sugary or starchy kernels of the same ancestry, (see p. 159) but also intermediates are relatively more numerous in the offspring of the so-called extracted recessives and of the mixed starchy and sweet ears (about 3 per cent) than in the offspring of the kernels that gave so-called extracted dominants (only .6 per cent). In the so-called extracted recessive ears of the F_3 taken by themselves there are about 5 per cent of intermediate kernels. Selected intermediate kernels give a higher percentage of intermediates, but intermediates occur in not inconsiderable numbers in both so-called pure extracted dominants and extracted hybrids, more in the latter than in the former. It would seem that the sweet character is in less stable equilibrium, so to speak, than the starchy character and that sweet types are more likely to vary toward starchy than are starchy types toward sweet types. The intermediates are not merely chance variants diverging with equal frequency from both starchy and sugary types. This is a tendency of the same order perhaps as that which has been observed by Collins and Kempton, who find as noted an excess of starchy over waxy kernels in their crosses of these types.

It is generally recognized that the starchy kernel is the more primitive type of corn and that the sweet races have been derived from the starchy races, though the whole process is prehistoric and there are no positive records, so far as I am aware, of the origin of a sweet race from a starchy race where the possibility of crossing

was excluded. To obtain a starchy race from a sweet race is much easier. I have practically pure flint ears, as far as appearances go, from the above described cross of Ruby Sweet and Black Mexican.

It is worthy of note here that from this dent sweet corn cross quite a percentage of flint kernels appear. East has also noted this fact in a similar case and regards it as showing that Black Mexican Sweet had a flint corn in its ancestry and carries latent flint. He believes that the sweet corns are of two groups in this respect, derived respectively from dent and flint ancestries and that their behavior in crosses with dents and flints will indicate to which of the classes they belong. In view of the fluctuating character of both sweet and starchy characters in crosses such a contention is difficult to test. As bearing on the whole question as to the significance in practical breeding work of the occurrence of fluctuating variants between the parental types in crossing it is worth while to quote here the final paragraph of a recent paper by Kempton ('19), based on his own and Collins's work on the inheritance of endosperm characters in corn.

> For the breeder of crop plants where most of the desired characters are almost infinitely complex, seldom alternative, and often intangible, Mendelism seems to have little of practical value to offer, whether the attempt of some investigators to so extend the theory as to embrace such characters be approved or not. While Mendelism may assist in making desired combinations, there is nothing to show that it can serve as a substitute for selection either in finding the best stocks or in preserving them from subsequent deterioration.

Collins and Kempton have perhaps done more than any others to broaden our knowledge of the behavior of corn in crossing, and the above statement is particularly interesting in view of the sweeping generalizations found in such a book as that of Babcock and Claussen.

2. PAIRING OF PARENTAL CHROMOSOMES, REDUCTION DIVISIONS, AND SEGREGATION

The occurrence of intermediates need not as noted lead us to question the cytological evidence for the segregation of the chromosomes from the male and female parents respectively in the reduction division and the chance recombination of these chromosomes in the succeeding fertilizations. The cytological

evidence for pairing of the homologous chromosomes from the two parents as indicated by length and other differential characters is accumulating rapidly both for plants and animals. For data as to plant material see Strasburger ('05), Stomps ('10) and Clemens Müller ('09 and '12).

While we need more convincing proof of the relationship of the processes in the so-called first and second divisions to the process of the reduction of the chromosome number there can be no question now that in general the sporophyte is a double or combination individual and that the chromosomes contributed by its two parents maintain a sort of individuality even when so combined.

Cytological evidence is as yet quite lacking as to just when and how in fertilization or in the succeeding divisions the homologous chromosomes are able to find each other out and attain the paired relationships which the sporophytic division figures show so clearly. Sax ('18) reports for *Fritillaria* and *Triticum* that they do not pair in the first division of the fertilized egg. Resort to conceptions of chemical affinity, magnetic polarities, etc., are of course useless here and our best suggestions, as it seems to me, are found in the conception of permanent connections or space relations between chromosomes and the mechanically active kinoplasmic elements of the colloidal cell organization which are indicated in Rabl's figure ('89), the constant relations between centrosome and nucleus observed by Conklin in *Crepidula* ('02) and the visibly permanent connections found between central bodies and chromosomes in the ascus ('97).

The pairing of the germ cells with each new fertilization is determined by the external environment and is a matter of chance, but the homologous chromosomes of each probably become paired through the mechanical activities made possible by the cell organization constituting the internal environment of the cell elements. We arrive here at a more precise conception of what may constitute the internal environment of the germ plasm than has hitherto been possible, though the assumption of an effective internal environment has seemed necessary to many on other grounds as well.

However the pairing may be brought about, there is general agreement that it has been achieved completely at synapsis and

for plants at least the visible appearance of the synaptic knot and the succeeding pachyneme spireme suggest that at this stage the chromosome pairs may become very intimately combined (Allen '05). On *a priori* grounds it would seem unlikely that such complex and labile compounds as we may suppose constitute the germ plasms should enter into such close physical relations of fusion without a greater or less amount of mixing and interaction which would more or less permanently alter their character. That the degree of such interaction should be the same in every case even of the same cross would seem to be quite improbable. It would be natural enough that many grades of interaction might occur in the synaptic stages leading to the formation of the eggs on a single ear of corn or the pollen grains of a single anther sac. The possible variability suggested by the cytological data as to synapsis forms a natural parallel to the variable degrees of mixing of the sugar and starch characters shown in the F_2 hybrid ears, resulting from the pairing of gametes from sugar and starch corns in the F_1.

3. RELATION OF SEXUAL REPRODUCTION TO VARIATION

If corn endosperms could be reproduced vegetatively such intergradations as we are discussing would doubtless occur as bud variations, like those Stout has described for *Coleus* ('15), but it is of importance to note that here they regularly follow sexual reproduction and it seems to me are to be regarded as the natural expression of the likelihood that processes so complex as we now know those of sexual reproduction are, should result in a higher percentage of variants than results from purely vegetative reproduction involving in the last analysis only nuclear and cell division. We need perhaps further careful statistical studies like those of Stout on species like *Coleus*, which can be propagated in both fashions to determine the relative frequency and degree of bud variation as compared with variation in sexually reproduced progeny. As it is we have the experience of commercial growers that in many cases in which seed progenies are quite variable progeny produced vegetatively by cuttings, etc., are sufficiently constant to be a reliable means of introducing and propagating important types of fruits and vegetables. No one questions that it is in general regarded as much easier to establish and fix a new variety which

can be propagated vegetatively than one which can only be propagated by seed. It seems to me that the evidence suggests that the general occurrence of intermediates as a result of crossing is due not only to the bringing together of divergent or contrasting pairs of characteristics but to the exigencies of sexual reproduction itself. It is easy to say that the combination of two equivalent things cannot result in variation but aside from the question as to whether male and female gametes ever are equivalents in any very strict sense it seems also obvious that the pairing of such complex colloidal systems as are the germ cells constitutes for each of the two individually as well as for the diploid unit which is coming into being an especially critical stage whose end result may very well show considerable fluctuating variability and in turn result in fluctuating congenital variability in the progeny.

An ear of corn with its large numbers of easily preserved and studied individual examples of such fusions produced under conditions involving a minimum of environmental variation is very favorable material for the recognition of such fluctuations. To be sure ears of pure bred races may show striking uniformity in their kernels especially in the starchy races but in the sugar corns variations in the degree of wrinkling are as I have found by no means rare occurrences. We must recognize without doubt as has long been obvious to the systematists fluctuating variability in the character of species as to their tendency to constancy or variability in their seed progeny. Some species or races show a high degree of fixity of type while others are just as truly characterized by their variability. There is nothing inconsistent with such facts in what we know of the relative fixity of the physical characteristics of various substances in the colloidal condition and of colloidal systems made up of varying proportions of the different elements or of different colloids.

What is true however of the chances of fluctuating variability in the offspring of gametes from individuals of the same so-called pure race is doubly true in the case of crosses between races differing in one or more characters. That the pairing of germ plasms from congenitally different parents should regularly and in every species result merely in a shuffling of fixed unit factors is out of harmony with what we know of the ordinary behavior of such viscid

colloidal aggregates as the gametes and the chromosomes when brought into such intricate relations as are the elements of the homologous pairs of chromosomes in the synaptic knot and the subsequent pachyneme spireme. Speaking in terms of chemistry and molecules no chemist would expect to be able always to isolate in a pure state by physical means alone such complex and unstable compounds as the proteins after they have been so intimately combined.

It seems to me necessary here to keep in mind always in connection with our theories of heredity and the structure of the germ plasm the known facts as to such polyphase colloidal systems as the cells appear to be. That the homologous chromosomes do pair, combine in the synaptic knot, separate in the reduction divisions, live a longer or shorter independent existence in the gametophytic generations, and then become paired again sooner or later as a result of gametic fusion are facts established from cytological observations and confirmed in their broad outlines by the evidence from breeding experiments for segregation and chance recombinations of characters. That however the germ plasms remain unaltered through these reproductive processes is not shown by breeding results and is quite inconsistent with what we should expect to be the results of the observed cytological processes on the viscid colloidal materials of the gametes as wholes and on the chromosomes themselves.

As noted corn with its large number of individual endosperms showing characters easily studied which can be obtained simultaneously and in parts of the ear under practically identical environmental conditions though each is the product of a distinct, free, and chance-determined pollination (in selfing so far as the variations in pollen of the same individual is concerned, in open pollination so far as variation of pollen occurs in the whole field) affords very special advantages for the study of variation both within a race and in hybrids.

The difficulty in distinguishing between variations which are due to environment and those which are germinal and congenital largely disappears in the case of these endosperm characters. Aside from the peculiar and apparently epigenetic cases of the pitted and chimaera-like kernels, it is easy to distinguish the

relative effects of environment and heredity on the form of the kernels and the degree of the wrinkling. Kernels at the butt of the ear tend to be smoother as a result of extreme pressure from the husks in this region. The kernels at the tip also show the effects of exposure if the husks are too short or of pressure if the husks are long and heavy, so that a well filled ear in its longitudinal growth meets considerable resistance from them. The hundreds of kernels in the middle region of the ear relatively to each other have a remarkably constant set of conditions through the whole of their development and the variations in their form are very obviously from their chance distribution to be interpreted as the expression of the exigencies of the fusion and pairing processes of fertilization, plus the particular and general qualities of the gametes which fuse and the chromosomes which pair. It has been too commonly assumed that the variations in the progeny of a pure race or the progeny from the crossing of two pure races must be largely if not wholly due to the external environment. With our increased knowledge of the complicated processes which are involved in synapsis, the reduction divisions, gametic cell fusions and the final pairing of homologous chromosomes it is obvious that at each and all of these stages there are abundant opportunities for variations in the germ plasm arising both from the chemical and physical interactions of the complex and labile materials of the chromosomes upon each other and of the cytoplasm, spindle fibers, etc., upon the chromosomes. As a single illustration take the frequently observed and figured cases of the occasional chromosome pairs which for one reason or another remain for some time connected in the equatorial plate and are tremendously elongated and distorted in being pulled back to the poles. In any theory of their nature and structure there is at least a chance that such a pair have been modified in some way and are different than their neighbors either before or as a result of this special variation from the normal processes of chromosome separation. Their position in the daughter group of chromosomes is for a time at least visibly modified. With the discovery of the normal paired relation of the homologous chromosomes of diploid nuclei the whole matter of the space relations of the chromosomes with reference to each other, to the centrosome and

to the nuclear membrane is coming to be recognized as a problem of fundamental cytological importance. These interrelations of the cell structures constitute as I have pointed out a sort of internal environment for the germ plasm but an environment from which in my opinion it is inseparable and which determines continuously in a considerable degree its constitution. With the recognition that all protoplasmic cell structures are phases of a complex of colloidal systems the question as to whether all change must not of necessity originate in environmental influence largely loses its point. That the position of the chromosomes with reference to the plasma membrane may be of significance, has been already claimed by Swingle in his theory of zygotaxis ('11, '13). That such conceptions seem far less fanciful, as our evidence for the individuality of the chromosomes and the reality of their paired positions in the diploid cells becomes more positive, cannot be questioned. During the period of the maturation and fertilization processes the germ plasm is best protected from, because it is least dependent on, the general external environment and in view of the complexity of these processes the claim that all change must be initiated by influences from outside the organism can have little weight. Changes resulting from the functioning of the mechanism of chromosome pairing and reduction, and gametic fusions may well be characterized as due to the normal capacity of the germ plasm for congenital variation. I am not suggesting here any doctrine of spontaneous or self-caused change, but am only pointing out that the stages of embryo initiation, from their obscurity and our ignorance of them, have been either regarded as of no significance (Lamarckian emphasis on influence of external environment) or have been given an exaggerated and strictly theoretically conceived importance (doctrines of germinal variation) in initiating variation and even evolutionary advance. With our better knowledge, we now see, from the very complexity of the mechanisms concerned and the fundamentally new relations into which the gametic cells enter in the act of fusion, there may well result at least what we may perhaps properly call with Meehan and Cook ('19) the normal fluctuating variation of the organism.

We realize more fully now than Darwin did that the question as to whether sexual reproduction is in itself a source of variation

or a means of swamping out existing variations involves the consideration of the complicated and far reaching mechanical and chemical interrelations of the cell structures concerned in the preparation for, and achievement of, cell or gametic fusion and the pairing of the chromosomes. It is obvious that we must distinguish at least two somewhat independent sets of conditions which determine the character of the embryonic progeny in sexual reproduction. First, the degree of similarity or difference in the ancestry of the gametes which are to combine and, second, the very processes of synapsis, maturation and union of the gametes. To be sure each of these sets of conditions determines the other in large degree. First, the complicated nature of the processes of reproduction set a limit to the degree of difference allowable in the gametes beyond which even if fertilization occurs embryo abortion may at once follow. Second, owing to the complexity of the fertilization process the degree of compatibility in the gametes may influence the probable range of variation in the progeny as well as their general vegetative vigor and fertility or sterility when grown.

It seems to me probable that the constitutional differences in the gametes are more likely to be responsible for the wider and so-called suddenly achieved variations known as mutations, sports, monstrosities, etc., while the complex nature of the reduction, mating, fusion, and pairing prcesses may well be regarded as responsible for those fluctuating normal variations which it has been so much the fashion recently to confuse with the not directly heritable variations due to the external environment.

It is not at all impossible of course that external environmental conditions of temperature, and nutrition, toxic effects, etc., may influence the complex of reproductive processes and thus affect the degree of congenital variation. The demonstration of this, however, by such studies as those of alcoholism, malnutrition, etc., in their influence on the offspring of sexual reproduction have so far led to no very conclusive results.

It is clear then, it seems to me, that the cytological discoveries as to the nature of synapsis, chromosome reduction, gametic fusion and chromosome pairing indicate that fluctuating variation may be expected as a direct result of the complexity of these

processes. The congenital characteristics of a series of hybrid offspring from the same pure bred parents and produced at the same time are not to be expected to be identical. Offspring from inbreeding or from selfing in a so-called pure race may also show congenital fluctuating variations due to the inherent nature of the sexual processes and quite independent of the so-called racial purity of the parents as fixed by carefully controlled inbreeding.

The endosperm characters of corn are as noted especially favorable for the detection of such phenomena since we have here in the hundreds of kernels from the middle region of a good-sized selfed or inbred ear a series of offspring from independent matings developed to maturity under practically identical environmental conditions except perhaps for a slight progressive diminution in food and water supply as we proceed from the butt of the ear to its tip and a little more crowding due to the narrowing of the ear in some races. The effect of these factors on endosperm characters is apparently so slight as to be negligible. Variations between the kernels under these conditions are to be characterized from their time of origin as congenital and are to be expected to be more or less fully heritable as my results from selecting and selfing intermediate kernels between the sugar and starch characters show that they are.

It is easy to assign differences between flowers or leaves on the same plant or between peas or beans from different pods or from the ends of the pods as compared with their middle region to the effects of environment, but differences between peas or beans from the middle region of the same well-developed pod or between kernels from the middle region of a large, well-filled ear of corn must be congenital. In the corn especially it is possible to obtain numbers large enough from the same ear to study such variations statistically as I have done and arrive at the certainty of their fluctuating and none the less more or less fully heritable value.

A further advantage afforded by corn for the study of these fluctuating variations is found in the practical fact that these endosperm characters are permanent and the ears are easily stored and preserved for comparison with the new data obtained in each succeeding year. No other material I know of is so favorable in all these respects for the careful and quantitative study of the inheritance of variations.

In emphasizing the fluctuating variability shown in the inheritance of these endosperm characters it is not to be forgotten that commonly there are some F_2 kernels and some ears in which segregation is quite pure. By selecting these apparently Mendelian results may be secured, but it is just as true that there are always other kernels in which more or less mixture of the characters for sugar and starch has occurred, and by selecting these intermediates in larger proportions may be secured, and probably by continued selection pure races of intermediates can be produced. The possibility of the existence of equilibrium types is to be recognized, representing phases of greater stability in the germ plasm toward which fluctuations tend to converge. Breeders who in general terms report the confirmation of East's and Correns's results in corn have probably more or less consciously selected from the typical parental types in planting for the F_3 and succeeding generations.

4. Nature of the sugar and starch characters

The characters sweet and starchy are typically metidentical characters. The presence of sugars and dextrin gums in solution or in sols leads in drying out to shrinkage of the cell and an irregular outline just as the whole kernel becomes wrinkled and shrivelled. The presence of more solid starch grains packing the cells full prevents this shrivelling with loss of water and the cells and kernels remain plump and rounded. This is a case of a metidentical character expressing itself morphogenetically and giving characteristic form differences in a many-celled structure. So far as I know it is the only case of this sort so far noted, most metidentical characters being matters of color, taste, etc., and such properties as length of life, fertility, sterility, etc. The character starchy or sugary can be transmitted directly as such through the egg and male cell. There is no question here as to a method of its representation in the germ plasm. It need not be considered as represented in the germ cells by a factor or factors which are not fundamentally the same as the character itself in its expression in other cells. In a sugar corn, speaking broadly and so far as we now know, the endosperm cells tend to contain certain more soluble carbohydrates as storage products. In a starchy corn the endo-

sperm shows a tendency to produce starch in greater proportions as a reserve carbohydrate throughout the life of the endosperm cells. Such tendencies or qualities need not be conceived as represented but as actually present as such in the germ cells, and as coming to expression in varying degrees according to the position of the cell in the multicellular plant body and its corresponding opportunity for the formation of storage products. We of course need much further data, both histological and cytological as to the sweet and starchy kernels but no facts so far known are, as it seems to me, inconsistent with the conception of these characters as metidentical form qualities which can be classed with the metidentical color characters which are so common. That such form characters must be conceived as the expression of a definite number of unit factors invariable except for relatively rare and strongly marked mutations, seems to me quite contrary to the evidence as it exists. The fluctuating behavior of these characters with the presence of all possible intergradation from the extreme of starchy to the extreme of sweet, as shown in FIGS. 167 *b*–167 *f*, suggests modification and fluctuating variability rather than mathematical fixity in the cellular basis of these characters. The fact that selection does not, at least at once, eliminate the extremes of the series of variants is opposed to the conception of such variability being due to recombination of multiple fixed factors. Typically starchy kernels and typically sweet kernels recur in the F_3 and F_4 generations, as is shown in the tables. The number of generations is small, but the case is one again in which the relative proportion of the varying types is changed by selection without the immediate elimination or the obviously proportionate elimination of variability. This series was not continued further, as other intermediate types seemed more promising for productiveness and other matters of interest. As noted above, further data will be given in connection with the description of such intermediates as a possible race of meal corns. All of the starch × sugar crosses which I have studied show in general a similar fluctuating variability, with a tendency to the inheritance of the intermediate condition when it appears. The intermediates obtained in the Wisconsin White Dent × Black Mexican Sweet cross may be taken as illustrative, so far as my

observations go, of the general behavior of the sugar and starch characters when crossed. The data as to small fluctuating but heritable variations as given by Jennings ('16), Stout ('15), Hegner ('19) and others, for asexual reproduction in pedigreed cultures has shown that the long recognized fixity of type resulting from asexual reproduction while sufficient in many cases to enable the horticulturist and practical breeder to furnish a fairly stable product for the market, is by no means absolute. Much more is it true as shown by Castle and Phillips ('14) for rats, Stout and Boas for flower number in chicory ('18), as well as in much of the older literature of the subject, that in sexual reproduction, we are concerned not with fixed unit factors subject only to relatively rare mutations, but with fluctuating variability probably increased by the special vicissitudes of cell and nuclear fusion and chromosome pairing and reduction. Certainly the current interpretation, except for Jones's paper, of the behavior of the sugar and starch characters in corn as due to a pair of fixed Mendelizing factors, subject to only rare and relatively unimportant mutations, has not been in accordance with the facts, even as they were shown by Correns's great paper.

DEPARTMENT OF BOTANY,
COLUMBIA UNIVERSITY

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Description of plates 3–5

Photographs and reproductions life size. Cards attached to the ends of the ears for pedigrees, data as to pollination, etc.

PLATE 3

FIG. 164 *a*. Kernels nearly all fully wrinkled and typical for sugar corn.

FIG. 164 *b*. Kernels showing many degrees of wrinkling but many of them tending toward translucency even when not fully wrinkled.

PLATE 4

FIG. 164 *c*. Kernels showing many degrees of wrinkling. The ear shows more opaque whiteness than 164 *b*.

FIG. 164 *d*. The ear though short has more of the appearance of the dent parent. Many kernels however are fully wrinkled and translucent.

PLATE 5

FIG. 164 *e*. The kernels are coarser and with much opaque white. Many of them quite of the dent type. Others are quite fully wrinkled.

FIG. 164 *f*. The ear was partly shelled by birds. It shows plump flint-like kernels, dimpled dent kernels, and fully wrinkled translucent sugary type kernels, as well as intermediates.

Notes on the Jack Pine Plains of Michigan

W. L. McAtee

The Jack Pine Plains or Barrens of Michigan, like analogous regions elsewhere, are of considerable interest to botanists. That they are barren from the agricultural point of view is shown clearly by the number of abandoned farms in their outskirts and the total lack of farming population in their typically developed interiors. However, the word barren, without modification, should not be applied to the Pine Plains, for in them some plants reach their very acme of development. For example the jack pine, *Pinus Banksiana*, the characteristic tree of the Plains, unhurt by fire for a sufficient time, makes a noble forest. Such crops of blueberries and pin and choke cherries as are produced on the Plains are exceeded nowhere; the writer saw numerous choke cherry trees with branches bent to the ground with their loads of fruit. Botanists have reason to be thankful that the Plains are barren agriculturally, for to this fact is due their preservation in something like their natural state; and they harbor numbers of the most interesting plants of Michigan.

The characteristic plants of the Jack Pine Plains have been listed at least thrice;* the object of the present article, therefore, is not to catalogue the plants of the Plains, but rather to give an idea of the appearance of the region in general, and to indicate the nature of certain subordinate plant associations of the Plains.

Why the Jack Pine Barrens are called Plains is not apparent at first sight in some parts of the region; certainly in the Boardman Plains, Grand Traverse County, ravines are numerous and there are many basins containing lakes, some of which are deep. However, there are extensive areas of fairly level country and the region no doubt is a dissected plateau. In Crawford County

* Beal, W. J. 18th Ann. Rep. Hort. Soc. Michigan 1888: 52–54. 1889. Beal, W. J., & Wheeler, C. F. Michigan Flora (second edition). 30th Ann. Rep. Sec'y State Bd. Agr. 1892: 19–21. Beal, W. J. Michigan Flora (third edition). Fifth Rep. Michigan Ac. Sci. 1904: 16–18.

there are larger, essentially flat areas, but there are also long but low parallel ridges.

As in the case of other regions in the eastern United States called Barrens, the distinctive appearance of the Jack Pine Plains is due chiefly to unusually wide spacing of the arborescent vegetation, giving a pleasing open effect to the landscape. Upon closer inspection the humbler vegetation also is seen to leave an unusual proportion of soil surface uncovered. There is no turf, there are no thickets; to this extent then, the region is barren, even to its specially adapted inhabitants.

So far as seen by the writer the Michigan Plains may be divided into three types, grading in intensity toward the typical Jack Pine country. Chiefly about the margins of the Plains, but scattered elsewhere, are areas where the dominant tree growth is oaks and maples. In this type, pin and choke cherries, witch-hazel and willow are most abundant; all of these plants are scattered also in the other types. A second type of barren is dominated by two species of aspen, *Populus tremuloides* and *P. grandidentata*, and is better supplied with sand cherry, service berry and choke berry than the other divisions. The third and most characteristic type of barren is that dominated by the Jack Pine; it appears to have more bear-berry, New Jersey tea and bush honeysuckle, also, than the other types.

However, the undergrowth in all of these types of Plains is very similar. Brake, sweet fern, and blueberries are the dominant ground cover; under and between them are scattered, more commonly than other things, the following: trailing arbutus, wintergreen, ground pine (*Lycopodium complanatum* and *L. clavatum*) and reindeer "moss" (*Cladonia*). The keynote of the Plains vegetation is resistance to drought and fire. Most of the plants have long deep roots or persistent rootstocks, and Dr. Beal notes that of seventy of the most common plants, sixty-eight are perennials. There are few biennials and the only annuals seen in the Plains are scattered specimens of widespread weeds, which are introduced to some extent wherever man and his domestic animals penetrate.

As a contribution to a future complete enumeration of the Plains flora the following lists of plants collected or observed at various points are presented:

Boardman Plains, Grand Traverse County

August 23 and 26; September 2, 1919

Pteris aquilina, dominant
Lycopodium clavatum, common
Lycopodium complanatum, common
Pinus Banksiana, dominant
Danthonia spicata, the most common grass
Smilacina racemosa, uncommon
Unifolium canadense, scattered
Comptonia asplenifolia, common, sometimes dominant
Quercus alba, scattered
Quercus velutina, scattered
Polygonella articulata, common
Silene antirrhina, numerous in one weedy locality
Fragaria virginiana, common
Amelanchier sanguinea, scattered
Crataegus macrosperma, scattered
Prunus virginiana, scattered
Acer saccharinum, scattered
Ceanothus americanus, scattered in colonies
Helianthemum canadense, scarce
Epilobium angustifolium, common.
Oenothera biennis, one basal rosette seen
Chimaphila umbellata, scattered
Epigaea repens, common
Gaultheria procumbens, common
Arctostaphylos Uva-ursi, scattered in colonies
Vaccinium pennsylvanicum, dominant
Vaccinium ovalifolium, one large colony seen
Asclepias tuberosa, scarce and local
Melampyrum lineare scattered
Diervilla Diervilla, common
Campanula rotundifolia, sparsely distributed
Solidago hispida, fairly common
Solidago serotina, a few specimens, evidently introduced
Aster undulatus, common
Leptilon canadense, appearing sparsely as a weed
Laciniaria "scariosa" group,[1] sparsely distributed
Anaphalis margaritacea, uncommon
Krigia virginica, fairly common
Picris hieracioides, scattered.
Hieracium scabrum, common
Hieracium venosum, common
Lactuca canadensis, appearing sparsely as a weed

In more or less aquatic situations in this region, but not belonging to the plains, which are dry, the following plants of interest were observed or collected:

Ibidium cernuum
Parnassia caroliniana
Dasiphora fruticosa
Argentina Anserina
Sanguisorba canadensis
Ledum groenlandicum

Dulichium arundinaceum
Eleocharis tenuis
Scirpus heterochaetus
Rhynchospora alba
Cladium mariscoides
Juncus brevicaudatus
Juncus canadensis
Polygonum amphibium

Shores

Andromeda glaucophylla
Chamaedaphne calyculata
Gentiana Saponaria
Chelone glabra
Aster Tradescanti

Marshes

Sarracenia purpurea
Epilobium lineare
Cicuta bulbifera
Agalinis paupercula
Campanula aparinoides
Lobelia spicata
Bidens cernua

[1] Which includes numerous undescribed species.

Lakes

Potamogeton natans[1]
P. amplifolius
P. heterophyllus
P. perfoliatus
P. foliosus
P. pectinatus
Naias flexilis
Zizania aquatica[1]
Scirpus subterminalis
Nymphaea advena
Castalia odorata

Rivers

Potamogeton interruptus
Naias flexilis
Veronica Anagallis-aquatica

Manistee Plains, Crawford County

August 29 to September 1, 1919

Pteris aquilina, dominant.
Unifolium canadense, common
Populus grandidentata, common
Populus tremuloides, dominant
Comptonia asplenifolia, dominant
Aronia melanocarpa, scattered in colonies
Amelanchier sanguinea, scattered
Prunus pennsylvanica, common
Prunus pumila, scattered in large colonies
Prunus virginiana, common
Acer saccharinum, common
Epilobium angustifolium, common
Vaccinium canadense, dominant
Vaccinium nigrum, common
Melampyrum lineare, scattered in large colonies
Diervilla Diervilla, scattered in colonies
Campanula rotundifolia, scattered
Solidago hispida, common
Solidago nemoralis, common
Solidago puberula, common
Aster laevis, scattered
Erigeron ramosus, scarce
Carduus lanceolatus, about camp sites as a weed
Picris hieracioides, scattered
Hieracium scabrum, common
Hieracium venosum, scattered

In wetter situations along the Manistee River were observed or collected the following additional plants of interest:

Clintonia borealis
Castilleja coccinea
Ledum groenlandicum
Aster puniceus
Aster sagittifolius

[1] Quantities of these plants have been transplanted to the lakes examined; *Chara*, *Myriophyllum* and *Utricularia*, not identified specifically, also were present.

INDEX TO AMERICAN BOTANICAL LITERATURE

1910–1920

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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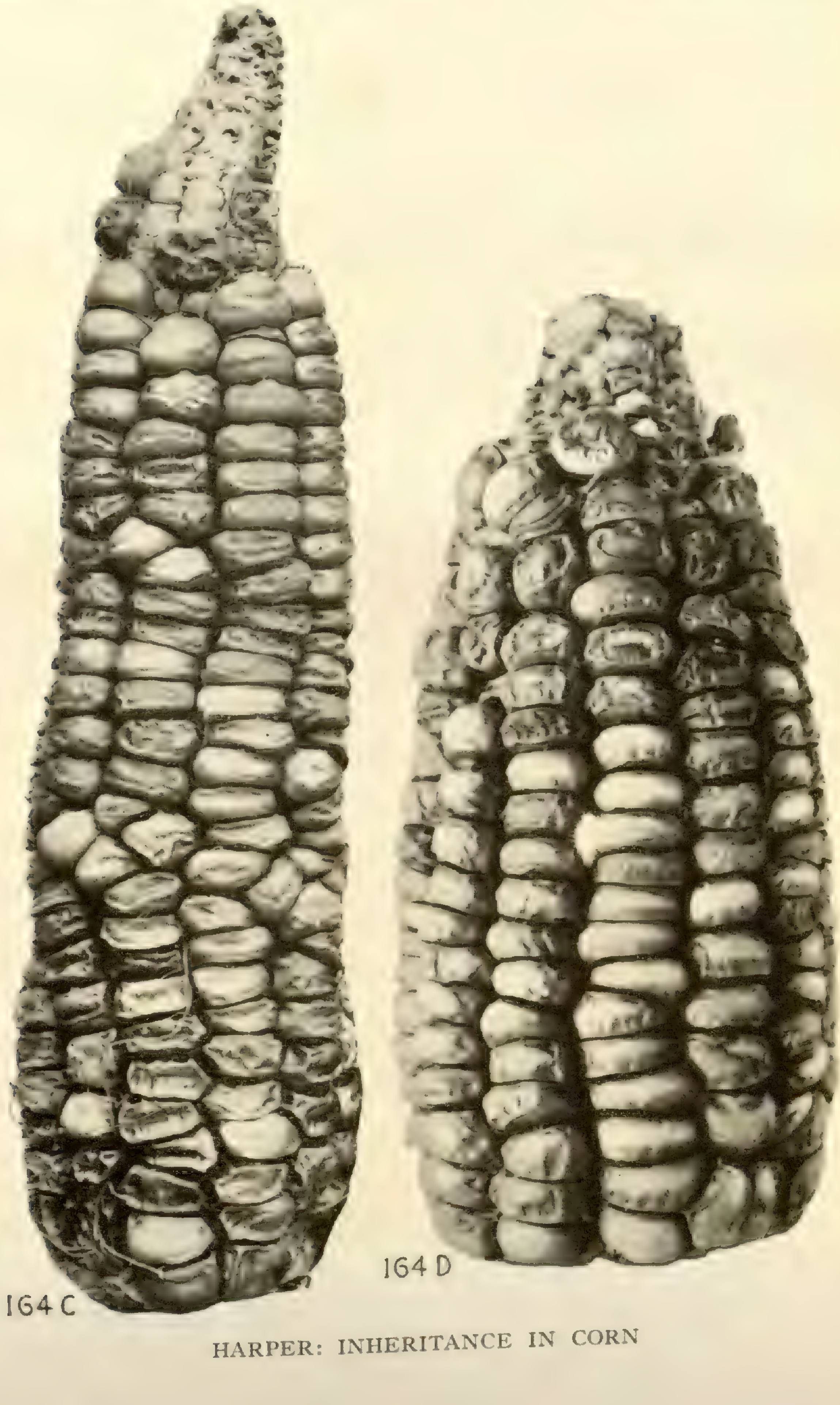
HARPER: INHERITANCE IN CORN



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HARPER: INHERITANCE IN CORN

Vol. 47 No. 5

BULLETIN

OF THE

TORREY BOTANICAL CLUB

MAY, 1920

Studies in the genus Taraxacum

HARVEY E. STORK

(WITH PLATES 6 AND 7)

LOSS OF SEXUALITY IN TARAXACUM

The genus *Taraxacum* presents some interesting problems—taxonomic, cytological and genetical. The classical castration experiments by Raunkiaer (7) in 1903 showed the common dandelion, *T. vulgare* (Lam.) Schrk. (*T. officinale* Weber), to be capable of setting viable seeds without pollination. Since Schwere (10) had previously described the development of the embryo from the egg cell, the condition was spoken of as "parthenogenesis," and Raunkiaer concluded that all species of *Taraxacum* were parthenogenetic. This was questioned by Dahlstedt (2) in 1907, and two years later Rosenberg (9) showed *T. confertum* to be normally sexual. Likewise, Ikeno and Osawa (6) showed that of two species growing side by side in Japan, *T. platycarpum* Dahlst. and *T. albidum* Dahlst., the former is normally sexual while the latter requires no pollination for the production of viable seeds.

Up to 1915 two careful studies had been made as to megasporogenesis and other cytological features in the genus: that of Juel (5) on *T. vulgare* and that of Osawa (6) on the two aforementioned Japanese species. At that time it was suggested to the writer by Professor D. M. Mottier that species of *Taraxacum* growing in America ought to be investigated. Accordingly, in the spring of that year, the writer commenced the study of the genus and was able to confirm the cytological work of Juel on

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T. vulgare. Several varieties of our common dandelion found growing in southern Indiana were drawn into the study, and although the material was selected from different varieties, the numerous preparations showed no differences in cytological behavior.

A second species, *T. erythrospermum* Andrz., has extended itself westward and finds a fairly general distribution throughout the middle western states. The sporogenesis of this species was likewise studied and the details of its megasporogenesis are given under a separate heading in the third part of this paper.

Meantime, numerous castration experiments after the manner first employed by Raunkiaer (7) were applied to plants of several varieties of *T. vulgare* and of *T. erythrospermum*. The object here was to determine whether all these forms set viable seeds in the absence of pollination and whether these show the same percentages of viability as seeds normally developed. The latter species had not been investigated in this respect up to that time. Raunkiaer had included a "*T. erythrospermum*" in the list of plants studied by him, but Dahlstedt (2) says that under this name was meant *T. laetum* Dahlst. Since that time Sears (11) has reported similar studies before the Ohio Academy of Science. In the experiments the excised part of each head was examined to make sure that the anthers were all closed and completely removed together with the stigmata. If this was not the case the entire head was discarded from the experiment. When a head was chosen that was too young, the result was that it dried up from too rapid a loss of moisture from the cut surface, especially in drying weather. It was therefore necessary to select heads at as late a stage as possible but before the opening of the loculi of the anthers. When these precautions were taken, the heads in all cases developed achenes altogether normal in appearance. Germination tests were made with seeds so produced and those produced in heads not castrated that grew by their side, in each case on the same plant. The seeds of *Taraxacum* will germinate immediately after they are mature. The results of these tests indicated no difference in viability between seeds normally developed and those from castrated heads.

Incidentally it may be said that seed formation in *Taraxacum*

vulgare is not easily interfered with. A small percentage of viable seeds were found in heads that had been cut down at the time of their flowering and left to lie in the grass. And if flower heads with their long scapes attached were cut from the plant and put under a bell jar in the laboratory, the achenes would complete their development and a small percentage showed germinability.

The question naturally followed, does normal fertilization ever take place in these species? The pollen of the two species shows great variation in size even within the same anther. In its development it shows such abnormalities as are often seen in the pollen formation of sterile hybrids. The degree of this abnormality varies in different plants. Numerous examinations of stigmata with pollen adhering to them were made under magnification for evidence of pollen tubes. None were ever observed in either species. The media used by various workers to induce the germination of pollen were employed in an effort to produce pollen tubes, but without result. Finally, numerous pistils, collected at a time just before their wilting, were fixed, embedded in paraffine in bundles of fifteen to twenty and sectioned for a short distance from the stigmatic end. After staining, careful examination revealed no trace anywhere of an invading pollen tube. All this, to be sure, cannot be considered conclusive evidence that the pollen does not germinate and that fertilization never takes place in *T. vulgare* and *T. erythrospermum*, but it points toward that conclusion. In this connection, Dahlstedt (2) expresses the opinion that in species generally "apogamous" there may occur single embryos arising normally from a fertilized egg. He refers to the results of Rosenberg (8), who found in the same head of a *Hieracium* "Apogamie" as well as fertilization.

It was found, as will appear in the cytological part of this paper, that there is no reduction division in the course of megasporogenesis. Enough embryological preparations were made to show that the embryo develops—at least usually, for it was true in all observed cases—from the unfertilized egg, which retains the $2x$ chromosome number. In a sense, it is an inaccuracy to call this cell an egg, for it lacks the character of a true egg of having the haploid chromosome number. For the same reason the term parthenogenesis cannot well be applied unqualifiedly to

such a case. The term apogamy, so far as its inherent meaning goes, applies, but this term has received a special significance by being applied to embryo-origin from a vegetative cell. Both terms are therefore objectionable, and the difficulty is due to the fact that the embryo starts from a cell that partakes of some of the characters of an egg and some of the characters of a vegetative sporophyte cell, more especially its diploid chromosome number. An arbitrary compromise was therefore reached by Winkler (12) in the adoption of the expression, "somatic parthenogenesis." It would seem to the writer much more logical to qualify the meaning of the term parthenogenesis by the use of the more specific adjective, diploid, instead of by the general adjective, somatic, for it is only that one character of a somatic cell, the possession of a diploid chromosome number, which one wishes to emphasize in connection with this type of apomixy. In all its other characters it certainly is not somatic. Sears (11) has coined the expression "amiotic parthenogenesis," The writer would characterize the condition either by the term "parthenogenesis" modified by an adjective, as "diploid" or "amiotic" or by the term, "ooapogamy." The latter term has been used, but the writer is at present unable to determine who is responsible for the expression.

Since the embryos of the two species of *Taraxacum* in question arise through ooapogamy, the reduced chromosome number does not enter into the life cycle of these plants and amphimixis is wanting. For this reason they suggested themselves as good objects for the study of certain genetical problems. Here the question of hybridization is completely shut out at the present stage in their evolution. It is possible that there was considerable hybridization at one time in the phylogeny of the genus. We must accept such a conclusion if we believe that polymorphy is the result of early hybridization. Did the ooapogamous species lose their normal sexuality independently of one another after they had arisen through hybridization, or did this loss occur in a single species, which is then the parent species from which were evolved the present-day ooapogamous species? Perhaps the latter of the two alternatives would seem the more likely, which would then mean that mutation had played a part in their production in the absence of hybridization. Dahlstedt

(2) remarks that "probably quite likely the genus has at one time been and is still perhaps in a period of mutation." It is believed that careful study, through cultures, of the plants of both sexual and apogamous species may throw some light on such questions as these. In whatever manner the ooapogamous condition arose, it was doubtless attended by an increase in the chromosome number, as will appear from the following table:

	Sexual forms		Ooapogamous forms	
	Haploid	Diploid	Haploid	Diploid
T. vulgare	—	—	13	26
T. confertum	8	16	—	—
T. erythrospermum	—	—	—	26–30
T. albidum	—	—	—	36–40
T. platycarpum	8	16	—	—

Perhaps the numbers under the ooapogamous forms should be spoken of as diploid and tetraploid, for it seems that the ooapogamous condition is attended by a doubling of the chromosome numbers. The higher figures may be inaccurate because of difficulties in making the counts of the small chromosomes, or the number may be irregular as an expression of the abnormal condition that exists. As Rosenberg (9) has pointed out, in all cases of ooapogamy in seed plants where chromosome counts are available, the ooapogamous species of a genus have a larger number of chromosomes than the sexual species, and the number is usually double. One striking exception occurs in the genus *Rumex*, which should be further investigated. The significance of this connection between ooapogamy and the doubling of chromosome numbers can be only a matter of speculation at the present time.

VARIATION IN TARAXACUM

Both *T. erythrospermum* and *T. vulgare* present great variability, and it is possible that the tendency to vary may be due to the large chromosome content. It would be interesting to know whether sexual forms with the 8 (16) chromosome-number show a similar tendency to variation. The literature gives us no evidence in this matter. With the chromosome content abnormally increased, one might expect mutations. Should a mutation

arise there would be no difficulty of its maintaining itself as a definite line, since hybridization does not enter as a disturbing factor. At the beginning of this work, it was conjectured that possibly some of the various forms of our common dandelion were fixed and that they would come true to type in the following generation. While they are often referred to, the writer has failed to find anywhere in the literature an explanation of the true nature of these various forms of *T. vulgare* and *T. erythrospermum*. The polymorphous condition has often been noted but definite explanations are wanting. For example, Sturtevant has deposited in the Cornell University Herbarium eight collections of *Taraxacum vulgare*, which he puts into five different varieties, differing from one another through a wide range of characters. Are such as these to be considered as fixed varieties, are they to be considered as variations called forth only for the immediate generation by environmental conditions, or are they fluctuating variations that have their cause within the plant rather than in the conditions of its environment? More than that, since the two species seem in their variations to intergrade so that it is at times difficult to say whether a particular form belongs to the one species or to the other, is *T. erythrospermum* perhaps to be considered merely as one of the numerous forms, a little more distinct than others, of *T. vulgare*?

To help toward a solution of these questions, cultures of the plants were resorted to. Dahlstedt (2) has already called attention to the necessity of cultures in the study of species of the genus and describes seven new species on the basis of cultures carried on in the "Bergianischen Garten" at Stockholm. In the summer of 1916 eight plants, determined by the writer as *T. vulgare*, were collected. These represented types of the most striking forms commonly observed and were selected with a view toward getting the greatest possible differences in leaf characters, size, involucral characters, etc. One typical plant of *T. erythrospermum* was also included as No. 9 of the series. From each plant one well-matured head was selected and the seeds of this preserved until February, 1917, when they were sown in pans of sterile earth in the greenhouse. In April fifty plants from each of the nine types were planted in rows in rich garden loam. In spite of

good soil and cultivation they grew but slowly during the first season. The rapidly-growing plants that one observes on lawns and in similar situations arise from old rootstocks. The seedlings do not come to flower the first year. They were covered during the winter and, in the following spring, started a rapid growth, developed to a large size and produced numerous flowers and blowballs during the season.

When the plants were quite young, the rosette leaves showed some variation in form, ranging from entire to deeply pinnatifid-runcinate. These variations did not follow the parent type forms but occurred among the members of the same race. As they grew older, greater uniformity resulted, and in the second season two distinct uniform types developed in the nine races. All the races, except No. 9 (collected as *T. erythrospermum*) and No. 6, gave plants that were striking because of their uniform conformance to one definite type, a large *T. vulgare* type with characters as commonly attributed in the keys, the leaves being up to 12 inches in length and the scapes up to 18 inches. So uniform were the foliage and flower characters that it was impossible to find the slightest variation to set one of the seven races off from the others. In striking contrast to these uniform rows were those of races No. 6 and No. 9. No. 9 had been selected as *T. erythrospermum* and gave a uniform race of plants somewhat larger than the parent plant but having the characters usually attributed to the species. Exactly like these plants were those of race No. 6, and it was a surprise to see that an error in determination had been made in the selection of this parent plant, a *T. erythrospermum* form having been mistaken for one of the *T. vulgare* forms, which only goes to show that the two so intergrade as to be sometimes, at least, indistinguishable. Sears (11) says, "both species possess such a wide range of forms that the only safe criterion for separating them seems to be achene color and form." And even these characters intergrade. There are dwarf forms of *T. vulgare* that have achenes conforming in shape, size, and spine characters to those of *T. erythrospermum*. The achene color varies from a light olive green to gray or brown and in some cases a red pigment is developed almost as distinct as in *T. erythrospermum;* while fruits of the latter species that have

matured in wet or cold weather often lack the distinct red color. It would seem then that to be sure in all cases of the identity of a plant, one must resort to cultures. In fact, so polymorphous are many of the species of this genus that it would be desirable to grow the species together in order to determine just what typical forms result under certain uniform environmental conditions. From what the writer has seen of some herbarium material named *T. palustre* (Sm.) Blytt nothing would indicate that it was anything more than a form of *T. vulgare*, like one of the seven kept under cultivation. Fernald (3) speaks of the difficulty at times of separating *T. palustre* from *T. vulgare* and says the former occurs in "damp sheltered situations, especially roadside ditches and similar spots," and it is in such situations that a variety of *T. vulgare* can at times be found having more or less the characters usually ascribed to *T. palustre.* Herbarium material has been studied of American plants named *T. lividum* (Waldst. & Kit.) Heller, *T. mexicanum* DC., *T. oblanceolatum* A. Nelson, *T. officinale alpinum* Koch, and *T. laevigatum* (Willd.) DC.; and similar difficulties are presented. Sears (11) concludes that the last of these is identical with *T. erythrospermum*, but the writer would hesitate to come to this conclusion from the varying herbarium material. The plants should be seen growing side by side. Dahlstedt (2) says *T. erythrospermum* belongs to the *T. laevigatum* group, and that if the whole group were to be made one collective species, the latter name would apply as having priority. In the preparation of his excellent monograph of the genus, Handel-Mazzetti (4) studied herbarium material of most of the species described as new in America, especially from the Rocky Mountain region and Canada, and placed most of them under definite European species.

The writer would welcome specimens with seeds from any of the species of *Taraxacum* found in America, in order that he might grow these together under similar environmental conditions and make some definite determinations as to just how far soil and climate are responsible for the varietal and specific or supposed specific differences in this genus. Moreover, such a collection of plants in culture would make possible further cytological and genetical studies which it is planned to carry out. The cultures

commenced in 1916 were interrupted during the two years of the war but are being resumed now.

MEGASPOROGENESIS IN TARAXACUM ERYTHROSPERMUM

The megaspore-mother-cell is a hypodermal cell at the apex of the nucellus and is easily distinguished by its denser staining. It rapidly increases in size, assuming an elongated form, and its large round nucleus attains a diameter not much less than that of a cross section of the cell. In the resting state, the nucleus show a large nucleolus (not more than one was ever observed) and a finely reticulate linin with densely staining chromatin. When entering the prophase, this reticulum becomes coarser by the merging of its elements, and the irregular strands soon contract into a dense mass—a typical synapsis (FIG. 1). Usually there are at the edges of the mass suggestions of threads, as appears in FIG. 1. Since this synaptic condition is encountered frequently in the preparations, it is reasonable to assume that it lasts a relatively long time. The spireme then loosens up until it is distributed again throughout the entire nuclear cavity. FIGS. 2 and 3 show stages in this process of loosening up, and FIG. 4 is drawn from a thin section of the nucleus when this stage is completed. The relatively thick thread appears to be of a finely granular nature. Nowhere in the preparations is there anything to suggest that the thread could be double at this stage. If it is a double thread, the two halves are so intimately merged as to be indistinguishable. In this stage *T. platycarpum*, which is a normally sexual species, is reported by Osawa (6) to present a clearly parallel spireme, while the ooapogamous species, *T. albidum* has a single spireme; neither does Juel (5) figure or describe a parallel spireme for *T. vulgare* at this stage. Osawa's figures seem very clear and definite in demonstrating the double spireme for *T. platycarpum*, and from the present known cases it would appear that the normal sexual *Taraxacum* species exhibit the double thread and the ooapogamous ones the single thread at the hollow spireme stage. It is interesting to note in this connection that Beer (1) doubts the existence of a double spireme at the hollow spireme stage in any of the Compositae that he has studied.

The thread now becomes shorter and thicker, the thickenings corresponding in number to the resulting number of chromosomes.

These thickened parts soon separate from one another (FIGS. 5 and 6) and are presently seen as irregular isodiametric chromosomes distributed throughout the nuclear cavity (FIGS. 7–9). At this stage counts are possible in thick optical sections. These counts vary from 26 to 30. No bodies are here observable that can be interpreted as its small nucleoli that Juel has described. The nucleus now gradually becomes elongated and, accompanying this elongation, the chromosomes undergo the remarkable change that Juel has described for *T. vulgare*, stating that it is a departure from all normal rules. This change consists in an elongation again of the chromosomes into irregular rod-shaped forms (FIGS. 10 and 11, the latter from a thin section.) These might be supposed to belong to earlier stages, like those shown in FIGS. 5 and 6, but the nature of the nucellus and the elongated form of the nucleus indicate that without a doubt this is a secondary elongation of the chromosomes after they had once assumed a more or less isodiametric form. The chromosomes here cannot be said to be in pairs except in so far as is brought about by chance, contrary to what Osawa reports for *T. albidum*. Nor does it seem possible that a splitting of the chromosomes here takes place, for there are certainly not upwards of 60 chromosomes in the nucleus at this time.

At this point the nucleus has become so much elongated that the larger dimension may be five times as great as the shorter (FIG. 12). The chromosomes again return to an isodiametric form and appear to be smaller and possibly denser bodies than when they first assumed this form. In the preparation from which FIG. 12 is drawn 31 chromosomes can be distinguished, though not with certainty. At this point the nucleolus and the nuclear membrane disappear, and one sees the spindle fibers make their appearance. The spindle is always regularly bipolar and in some cases is observed to lie at a considerable angle in the cell (FIG. 16). The wall between the resulting daughter cells is often also more or less oblique but never to so great a degree as was observed in the case of the spindle. Whether an abnormal shifting of the spindle was produced in some cases by fixation or other manipulation or whether the wall has a tendency to form in a position more nearly at right angles to the long axis of the cell is not known. The chromosomes are at first loosely scattered

over the entire spindle (FIG. 14) but soon move toward the equatorial plane and are there arranged in quite regular order (FIGS. 13, 15 and 16). Meantime the spindle shortens somewhat and has all the appearance of a spindle in a vegetative cell. In fact, it is frequently possible to compare it with a spindle in the vegetative tissue of the ovule in the same preparation and, except for the somewhat smaller size of the latter, no difference is to be observed.

The chromosomes now separate into halves and the anaphase is quickly completed. FIG. 17 represents the completed division. In the daughter nuclei the chromatin becomes arranged into an indefinite network, but the chromosomes do not immediately lose their identity in this network but remain as irregular enlargements (FIG. 18). The nucellus at this time gradually disappears. No second division takes place to form a tetrad. The chalazal daughter cell quickly enlarges to form the mother-cell of the embryo-sac while its sister cell degenerates and is crowded into a gelatinous cap. (FIGS. 19 and 20). At this stage the pollen in the same flower is mature, but the loculi are still unopened.

A single division of the megaspore-mother-cell takes place also in *T. vulgare*, and the same condition has been reported in the ooapogamous *T. albidum* by Osawa (6); the sexual species, however, *T. platycarpum* (6) Osawa, and *T. confertum* (Rosenberg, 9), show two divisions to produce tetraspores. From this it appears that with the loss of sexuality has gone the loss of one of the divisions of the megaspore-mother cell.

Material was fixed principally in Flemming's medium solution and stained with Flemming's triple stain, as used in Mottier's laboratory, though Haidenhein's haematoxylin method was also used. The use of turpentine, as recommended by Professor Mottier for bleaching after osmium fixers, was found almost indispensable in gaining clear preparations. My best thanks are due Professor Mottier for his kind help.

CORNELL UNIVERSITY.

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Explanation of plates 6 and 7

All the figures were drawn with the camera lucida. FIGS. 19 and 20 are magnified about 800 diameters; the remaining figures, about 1800 diameters.

PLATE 6

TARAXACUM ERYTHROSPERMUM Andrz.

FIG. 1. Megaspore-mother-cell with nucleus at stage of synapsis.
FIGS. 2, 3. Chromatin coming out of synapsis as a single thread.
FIG. 4. Thin section at hollow spireme stage.
FIGS. 5, 6. Segmentation of the thread into chromosomes.
FIGS. 7–9. Optical sections of nuclei with short thick chromosomes.

PLATE 7

TARAXACUM ERYTHROSPERMUM Andrz.

FIG. 10. Secondary elongation of the chromosomes.
FIG. 11. Thin section at same stage.
FIG. 12. Second shortening and thickening of chromosomes just prior to spindle formation, nuclear membrane disappearing.
FIGS. 13, 14, 15. Arrangement of chromosomes on spindle.
FIG. 16. Characteristic regular metaphase stage; oblique position of spindle in cell.
FIG. 17. Telophase with disappearing spindle.
FIG. 18. Daughter cells of first and only division.
FIGS. 19, 20. Later stages of same; upper cell in each case is the chalazal cell.

A new Oreocarya from Colorado

GEO. E. OSTERHOUT

Oreocarya procera sp. nov.

A biennial or short-lived perennial, stem 3–4 dm. high from a tap root, single or usually with some shorter stems from the base, green but hispid with horizontal, stiff, white bristles, though not densely so, and thinly covered beneath with short reflexed hairs; the lowest leaves spatulate, including the slender petiole about 5 cm. long, stem leaves oblanceolate, the middle ones 4–5 cm. long including the short petiole, and 3–10 mm. wide, densely pubescent on both sides with short close pubescense, and the lower side with stiff bristles, and the edges beset with stout bristles; floriferous from near the base, the flowers on short axillary branches, in somewhat capitate clusters which lengthen in fruit, alternate, and on some of the stems scarcely overlapping till near the top; the calyx lobes lanceolate, 4 mm. long, becoming 6 mm. in fruit, bristly; the corolla 3 mm. long, the limb 5–6 mm. wide, the throat crested, the anthers included, filaments very short; nutlets four, ovate, when mature about 3.5 mm. long, rather more than 2 mm. wide, margined, but not winged, bluntly tuberculate on the back, the tubercles more prominent on the slight middle ridge.

The only locality from which I have *Oreocarya procera* is Glenwood Springs, Garfield County, Colorado, where I have collected it on four different dates, and as I remember, in stony soil along the Grand River. The first collection was on July 1, 1895. For the type specimen I have chosen No. 1867, collected June 18, 1899. *Oreocarya procera* is tall and remotely leafy for an *Oreocarya*, and not so densely hispid as many of them. The somewhat immature nutlets appear to be narrowly winged, but the mature nutlets are only margined. It does not closely resemble any *Oreocarya* with which I am acquainted, but has a slight resemblance to *Oreocarya affinis* Greene.

Internal stomata in ericaceous and other unrelated fruits

H. F. Bergman

(WITH NINE TEXT FIGURES)

In the examination of some diseased fruits of the cultivated cranberry, *Oxycoccus macrocarpus* (Ait.) Pers., during the winter of 1918–19, the writer observed stomata in considerable numbers in the endocarp or membrane lining the seed cavity (FIG. 1). This condition seemed so anomalous that diligent search through the literature was made in order to find out if the presence of internal stomata had previously been noticed and, if so, in what fruits they had been reported. Very few definite statements relative to internal stomata were found. In the tulip, *Tulipa Gesneriana* L., Czech (1, p. 104) reported their occurrence on the margin of the seed, thus confirming (p. 106) an earlier observation of Th. Hartig, and stated that he had found them also on the inner side of an unripe capsule. Schleiden* had already seen them on the integument of the seed in *Canna*. Weiss (9, p. 385) makes the following statement concerning stomata: "dem Fruchtknoten fehlen sie fast nie und kommen auch in der Innerauskleidung desselben vor,† desgleichen auf der Testa der Samen." Tschirch (8, p. 437) writes as follows: "Spaltöffnungen finden sich überall an der Pflanze, wo die Epidermis erhalten ist, nur dem Wurzeln und den Endosperm fehlen sie ausnahmlos. Man hat sie selbst . . . an der inneren Fruchknotenwand . . . gefunden." Aside from these statements nothing bearing on internal stomata was to be found in the early literature. Within more recent times, however, Winton (10), from observations made during the study of the structure of various edible berries used for jams and preserves, records the occurrence of stomata in the epidermis of various fruits.

* See De Bary, Comparative anatomy of the vegetative organs of the phanerogams and ferns, English edition, p. 45, footnote, where the citation, "Schleiden, Beitr. p. 10," is given. Schleiden's work has not been seen by the writer.

† As a footnote here is cited "Krocker, H. De Plantarum Epidermide. Vratislaviae 1833.—'Sie kommen da ganz allegemeine vor.'"

With reference to the structure of the cranberry he states (p. 320) that "although stomata are entirely lacking in the epicarp, it is a remarkable fact that they occur in considerable numbers in the endocarp." He also gives a figure (p. 319, *f. 29*) showing characteristic cells of the endocarp with stomata. FIG. 1 shows a similar condition.

The question immediately arose as to the possible occurrence of internal stomata in other plants, especially in other Ericaceae. Dr. Neil E. Stevens, of the Bureau of Plant Industry, kindly loaned the writer some permanent slides of sections of the fruits of *Epigaea repens* L. An examination was made of a number of sections and stomata were found in the endocarp. At that time no other plants were available, and further observations were left until later.

Among the ericaceous plants which were examined during the summer and autumn of 1919 were wintergreen (*Gaultheria procumbens*, L.), bear berry (*Arctostaphylos Uva-ursi* [L.] Spreng.), Indian pipe (*Monotropa uniflora* L. and *M. Hypopitys*, L.), blue berries (*Vaccinium corymbosum* L., *V. pennsylvanicum* Lam. and *V. vacillans* Kalm), huckleberry (*Gaylussacia baccata* [Wang.] C. Koch), dangle berry (*Gaylussacia frondosa* [L.] T. & G.), mountain cranberry (*V. Vitis-Idaea* var. *minus* Lodd.) and mountain laurel (*Kalmia latifolia* L.). Other species studied were canna (*Canna* sp.), St. John's Lily, (*Crinum asiaticum* L.) and cultivated snowberry (*Symphoricarpos racemosus* Michx.).

In describing the endocarp of the blueberry Winton (11, p. 371) says: "This tissue, consisting of a single thin layer of loosely united stone cells, is intermediate between the parenchymatous endocarp of the cranberry on one hand, and the thick stone-cell tissue of the huckleberry endocarp on the other. These stone cells separate readily from one another and are remarkable for their diversity of size and shape." He shows also (p. 371, *f. 288*) a figure of the endocarp of a blueberry (*V. Myrtillus* L.) *without* stomata.

In the three species of blueberries studied by the writer stomata were found in the endocarp, although often much deformed. The stomata are largest in *V. corymbosum* (FIG. 2). In *V. pennsylvanicum* (FIG. 3) they are similar but somewhat smaller. The

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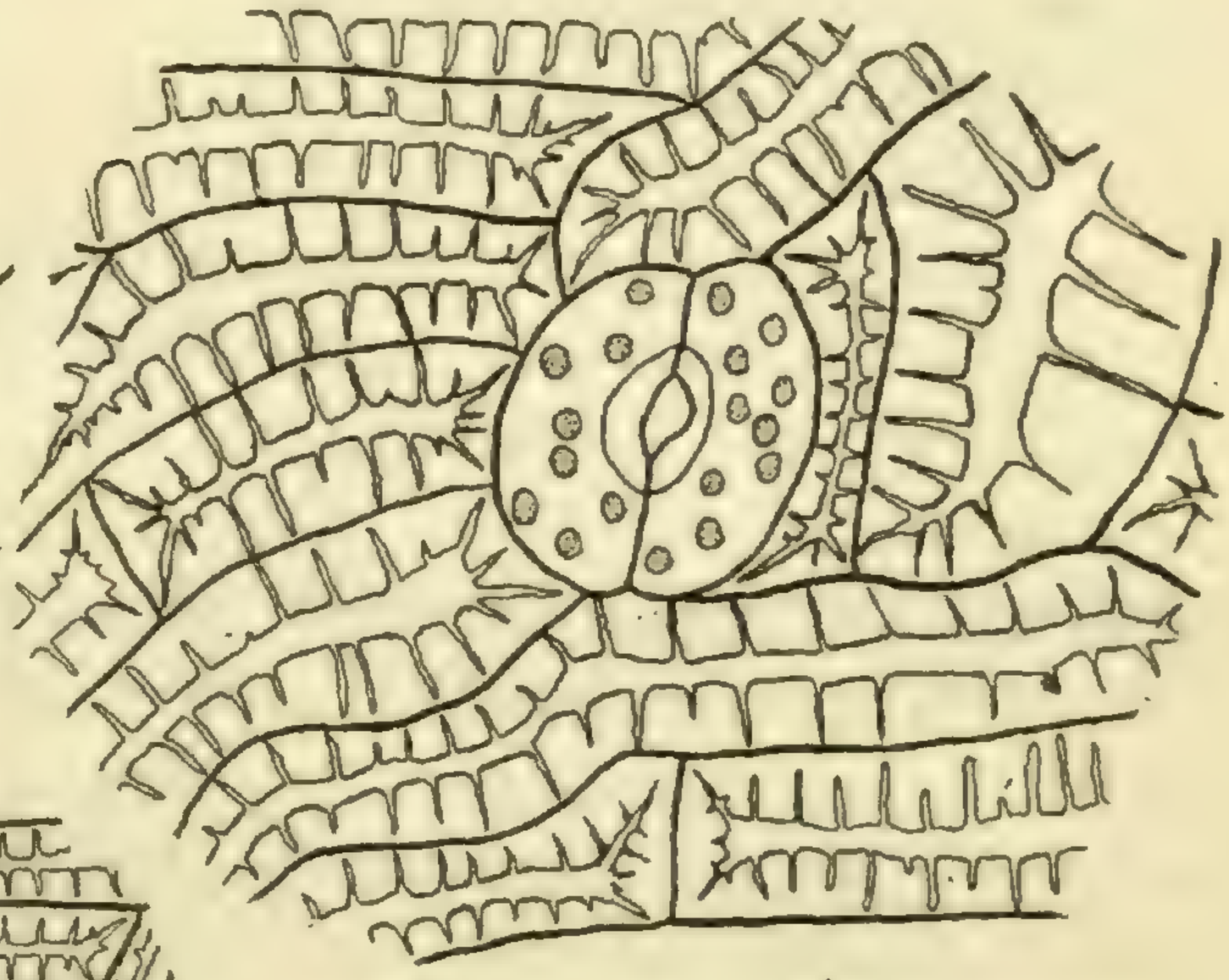
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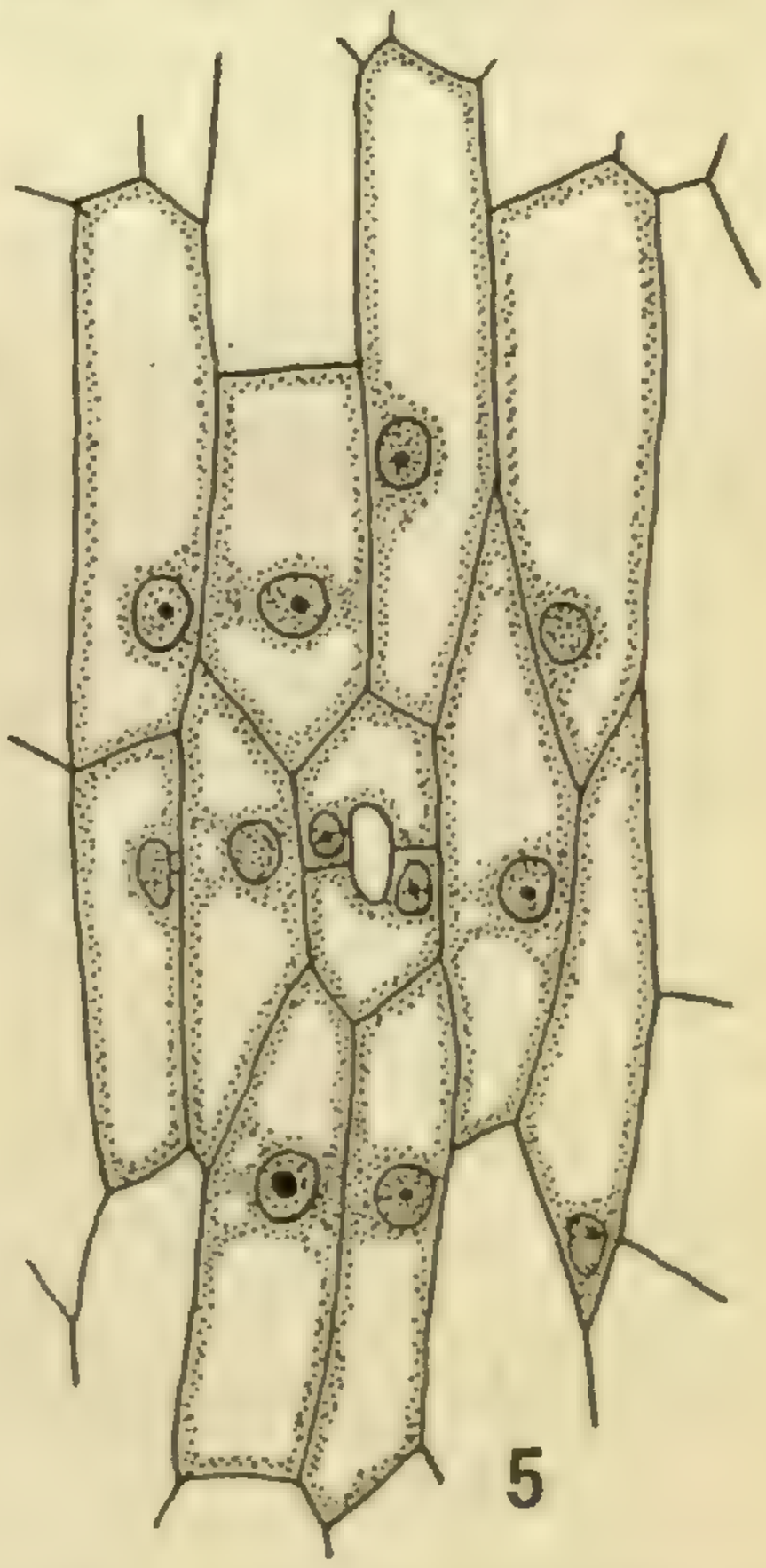
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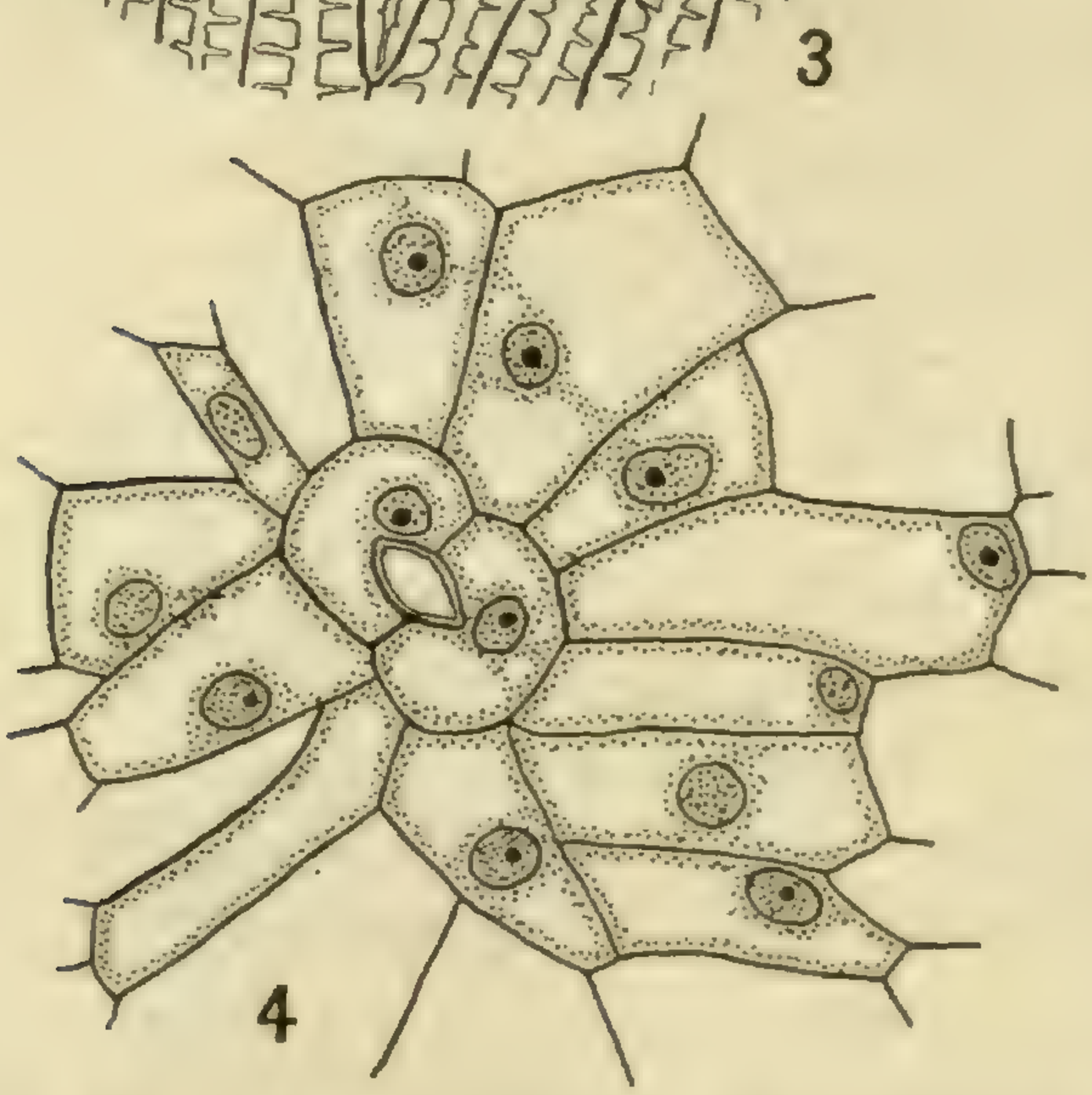
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FIG. 1. A group of cells from the endocarp of cranberry (*Oxycoccus macrocarpus*) showing a stoma, × 125.

FIG. 2. A portion of the endocarp of the swamp blueberry (*Vaccinium corymbosum*) showing a stoma, × 380.

FIG. 3. A portion of the endocarp of the low blueberry (*Vaccinium pennsylvanicum*) showing a stoma, × 240.

FIG. 4. A group of cells from endocarp of Indian pipe (*Monotropa uniflora*) showing a stoma, × 190.

FIG. 5. A group of cells from the under side of a scale leaf of Indian pipe (*Monotropa uniflora*) showing a stoma, × 190.

guard cells in all three species contain chloropasts. Stomata also occur in the endocarp of fruits of *Vaccinium Vitis-Idaea* var. *minus** and in the endocarp of *Gaylussacia frondosa*. The outline formed by the guard cells in the last species is generally typical, but the stomata seem to be less well developed than in *Vaccinum* and always closed. Both species of *Gaylussacia* have an excessively stony endocarp.

Almost all authors agree on the complete absence of stomata in *Monotropa Hypopitys*. Thus Rudolphi (5, p. 70) says, "sie fehlen . . . bei *Monotropa Hypopitys*, *Ophrys nidus-avis* and *Cuscuta Europaea*." This statement or a similar one may be found in many of the more important works on plant anatomy. On the other hand Porsch (3 pp. 78–79) quotes Chatin† as the authority for the statement that stomata occur rarely in *Monotropa*, although Chatin, in a special part of his work, asserts the absence of stomata on the stem and scale leaves. Chatin also, according to Porsch, reports the occurrence of stomata on the under side of the scale leaves of *Monotropa uniflora*. Solereder (7, p. 489) also says, "stomata are only met with exceptionally (and not in all the Monotropeae) on the axis or on the lower side of the leaf."

Observations were made on a number of plants of *Monotropa uniflora* without finding stomata in the endocarp or elsewhere. Plants of this species, however, collected in Livermore, Maine, July, 4 1919, by Dr. Stevens, showed occasional stomata in the endocarp (FIG. 4) and also on the scale leaves (FIG. 5). These were large and much misshapen, the aperture being often longer on the transverse axis of the stoma than on the longitudinal. Repeated observations of the inner surface of the ovaries of *M. Hypopitys* have failed to reveal the presence of stomata, although they have been found on the under side of the scale leaves.

Stomata were not found in the endocarp of *Gaultheria*, *Kalmia*, *Arctostaphylos*, *Gaylussacia baccata* or *Symphoricarpos*. Later, fruits of *Canna* and *Crinum* were examined and numbers of stomata found in the endocarp (FIGS. 6 and 8). The stomata on

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* Material collected by Miss Mary Percival on Mt. Washington, New Hampshire, August 10, 1919. Observations made by Dr. Neil E. Stevens.

† Chatin, Adolphe. Anatomie comparée de végétaux. Paris. 1856–62. Chatin's work has not been seen by the writer.

the integument of canna seed (FIG. 7) are peculiar in having the guard cells very much larger than the surrounding cells. The presence of internal stomata in fruits of the tulip and other monocotyledonous plants is of much interest, since these are very remote in relationship to the ericaceous plants, in which group internal stomata have been most often found. No further observations have been made as to the possible occurrence of internal stomata in fruits of other monocotyledonous plants.

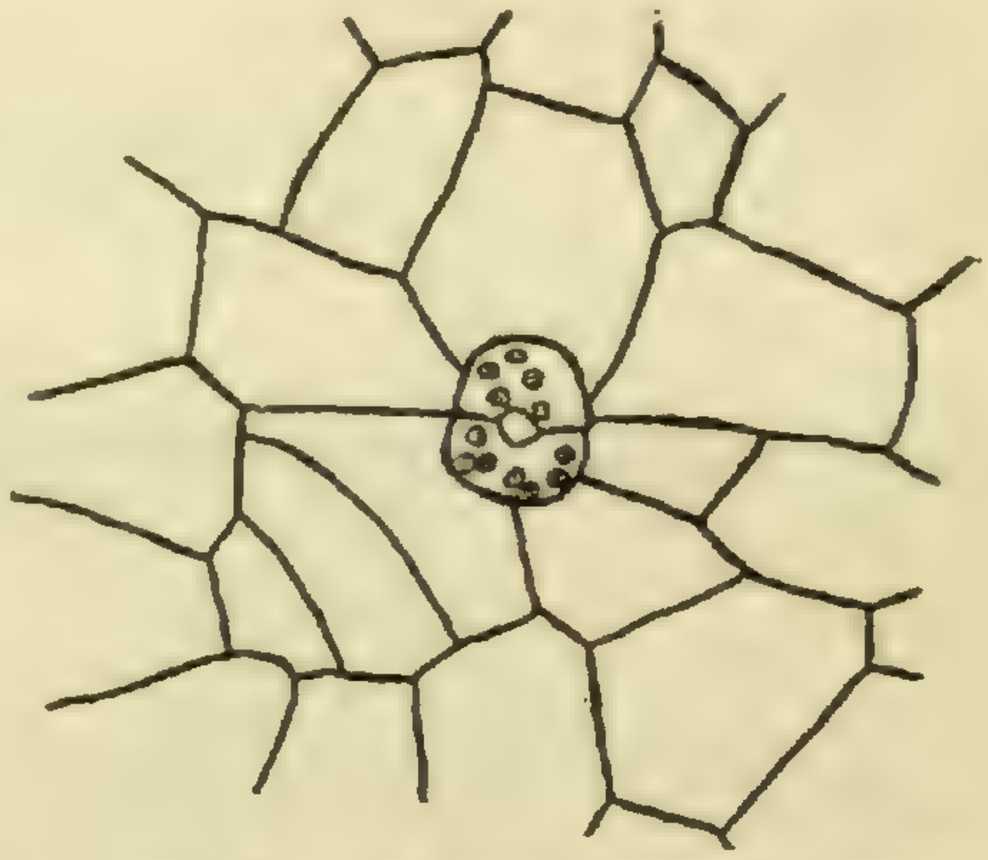


FIG. 6. A stoma from the endocarp of canna with adjacent cells, × 240.

Two points of great importance to be considered in connection with the presence of internal stomata are, first, to determine whether or not they retain their ability to function, second, to account for their persistence inside the fruit. In the attempt to answer the first question a number of observations have been

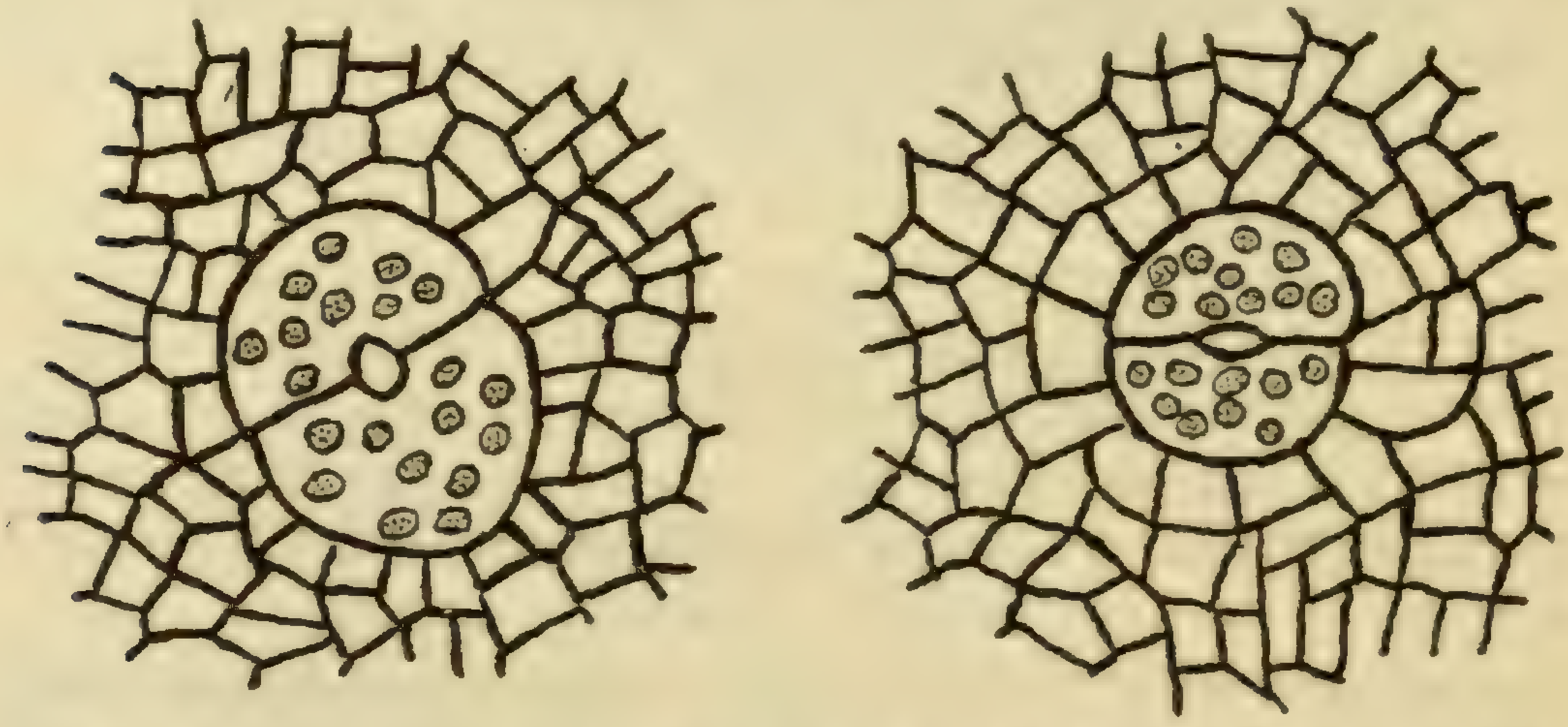


FIG. 7. Two stomata with adjacent cells from the integument of canna seed, × 760.

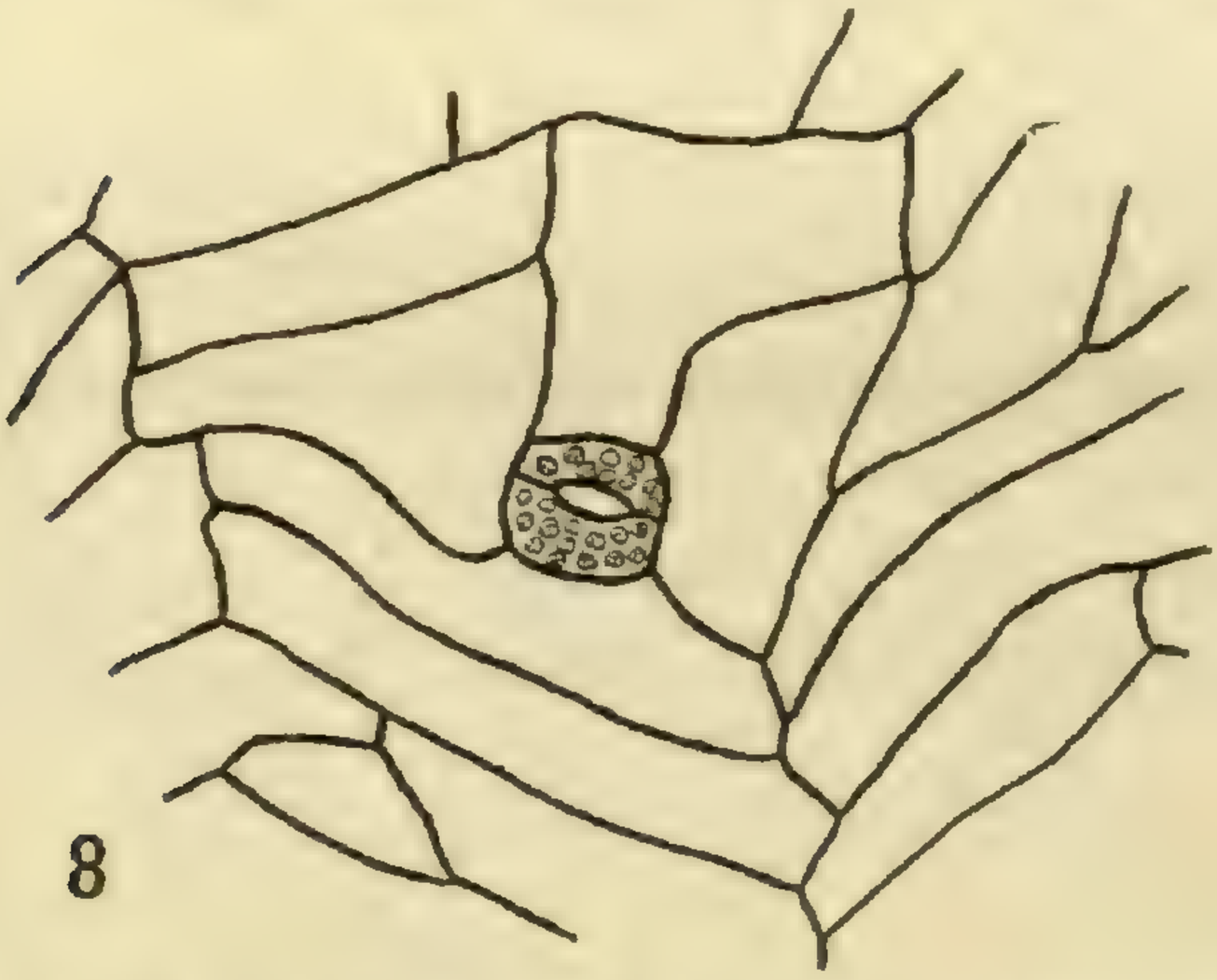
made on the cultivated cranberry. Berries freshly collected from the plants on clear days were taken at once into the laboratory and portions of the endocarp mounted and examined. Other berries were collected on densely cloudy days, when examinations of the stomata on the leaves of *Gaultheria*, *Arctostaphylos*,

Oxycoccus, *Maianthemum*, *Taraxacum*, *Trifolium hybridum* and *Plantago major* showed the stomata to be closed. It was found that the internal stomata in cranberries were open as fully when collected on cloudy days as when collected on clear days. Examinations of the stomata in the endocarp of cranberries were also made from material collected in the evening shortly after sundown. The stomata were open in this case also. Stomata of other plants at sundown were found to be nearly, if not completely, closed. Moreover, an occasional stoma in the cranberry may be closed, even when most of them are wide open. Apparently these statements apply also to the blueberry and *Monotropa uniflora*, for in the many examinations of internal stomata from these plants which have been made, the stomata have been found to be open in nearly all cases. Accordingly, it appears that the stomata remain mostly in an open condition and are not functional.

As the internal stomata in the specimens examined apparently no longer retain their ability to function, it remains only to account for their presence. Morphologically a fruit must be considered as a modified leaf or as two or more modified coalesced leaves with or without some accessory parts. From the natural position of leaves on the plant, it is to be expected that the upper side of the leaf would become the inner part or endocarp of the fruit.

It is to be noted, however, that in cranberries and most other ericaceous plants the stomata occur only on the under side of the foliage leaves. We have then the apparent anomaly of a twisting or reversal of position in the fruit. A comparison of the epidermal structure of the fruit with that of the upper leaf surface shows many similarities. The shape and character of the cells in surface view and in cross section show a heavy cuticularized outer wall. Similarly the lower epidermal cells of the leaf show a correspondence with the cells of the endocarp. As far as the similarity of the epidermis of the fruit to the upper leaf epidermis is concerned, it is without much doubt simply an analogy. The lower side of the leaf in becoming modified and transformed into the fruit would of course form the outside layer of the fruit. The epidermis of the fruit and upper leaf epidermis are both exposed to the same conditions and both must protect the plant from undue loss of water. Accordingly it is not surprising that a similarity in structure has resulted in response to identical factors of the environment.

The assumption that the leaf has reversed its surfaces without an actual turning on the axis might apply very well if the epidermis of the fruit only were considered. The explanation does not seem to apply as well to the endocarp. There is apparently no useful purpose which the stomata in the endocarp might serve and to assume that they have developed from a stomata-less surface without a demand seems absurd. There still remains the possibility that in the development of the fruit the leaves which enter into the formation of the carpels have actually turned on their long axis in the process of this transformation. No evidence can be submitted to substantiate either of these suggestions. They are merely offered and left for some anatomist to answer.



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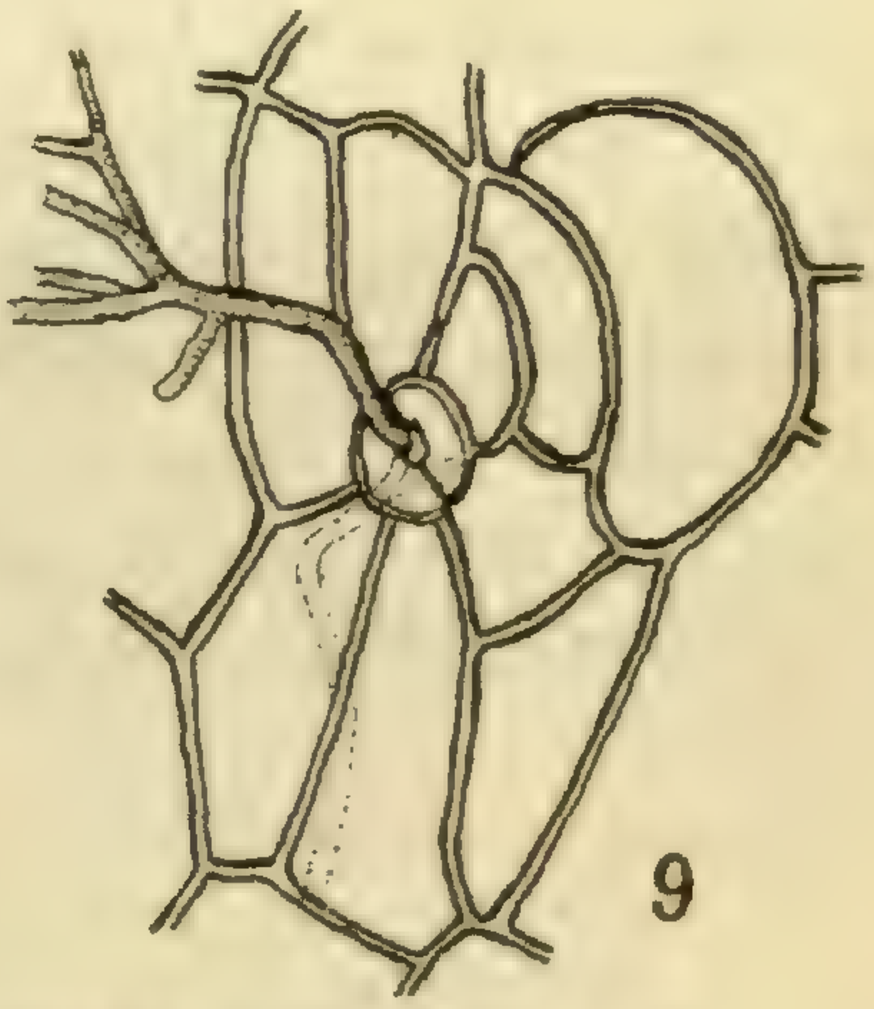

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FIG. 8. A stoma from the pericarp of *Crinum* with adjacent cells, × 190.

FIG. 9. A stoma from the endocarp of cranberry showing a fungus hypha which has come through the stoma and branched out in the seed cavity, × 240.

As these internal stomata apparently serve no purpose their persistence must be regarded as a hereditary continuation of a stomata-producing tendency after the leaf has lost its normal form and function. The persistence of stomata in parts where they are no longer useful is well known. Other examples of this are found in the occurrence of stomata on the axis and scale-leaves of underground stems of numerous plants observed by Hohnfeldt (2, p. 48) and in the persistence of stomata on submerged organs of many aquatic plants. Schenk (6) calls attention to the significance of heredity in explaining the occasional appearance of stomata on submerged organs as does also Porsch (4, p. 132).

It is of interest to note that in several instances in the examination of fungus-infested berries hyphae have been found entering the seed-cavity through the stomata of the endocarp (FIG. 9). This apparently was not accidental as it was observed in several instances and in no case were hyphae found which had penetrated the cell wall.

In conclusion a statement may be made with reference to gaseous interchange. It has been found that a rapid interchange of gas occurs in the respiration of cranberries and blueberries. These fruits have a thick epidermis in which stomata or lenticels are entirely lacking. The epidermis of the cranberry is provided with a layer of cuticle. That of the blueberry is cuticularized, although less so than in the cranberry. Whether or not the rate of respiration in fruits can be correlated with the thickness of the epidermis or with the cuticularized layer in the epidermis and whether a difference can be shown to exist in the rate of respiration of fruits with and without stomata are questions for further study. As stomata are lacking in many fleshy fruits most of which are provided with cuticularized epidermis, we have in such fruits excellent examples of gas interchange through cuticularized surfaces.

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INDEX TO AMERICAN BOTANICAL LITERATURE

1909–1920

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Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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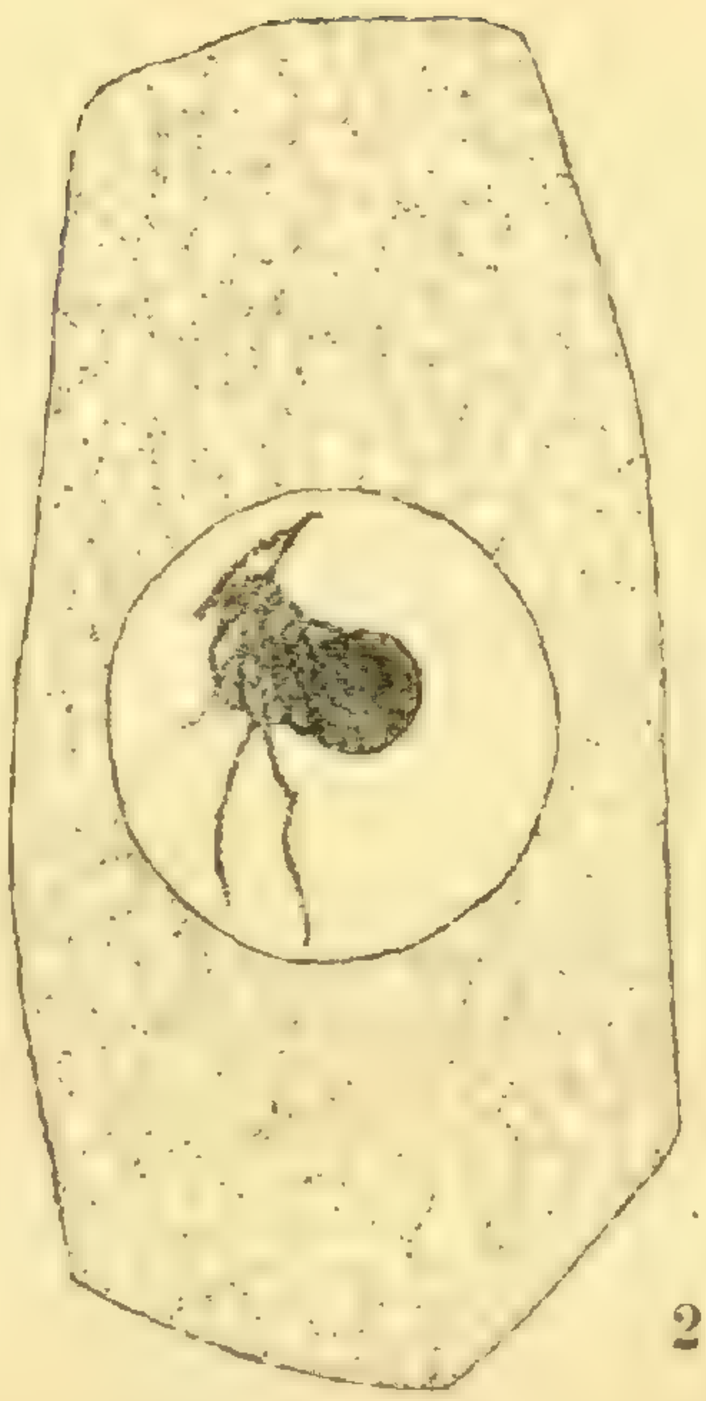

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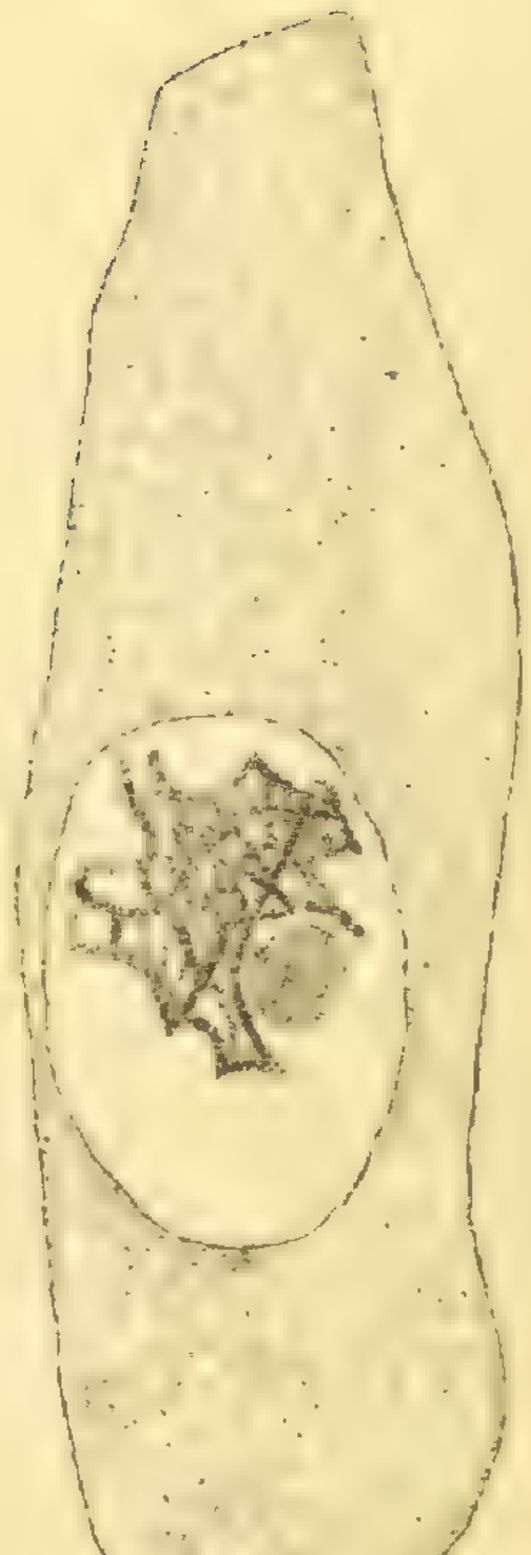

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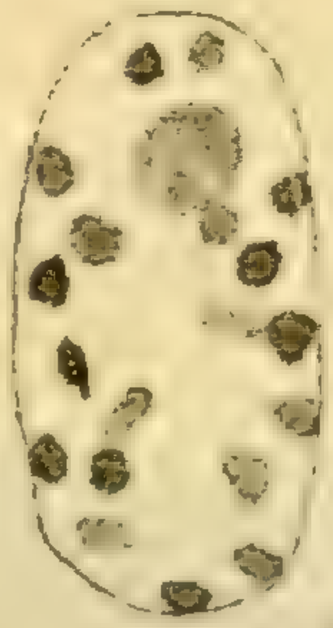

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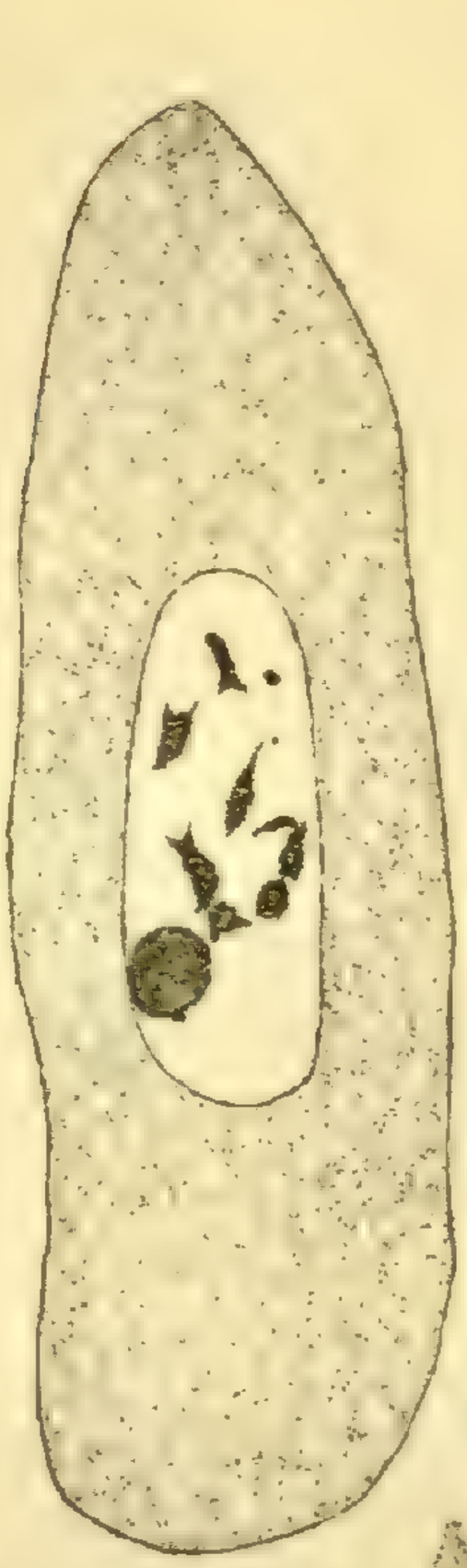

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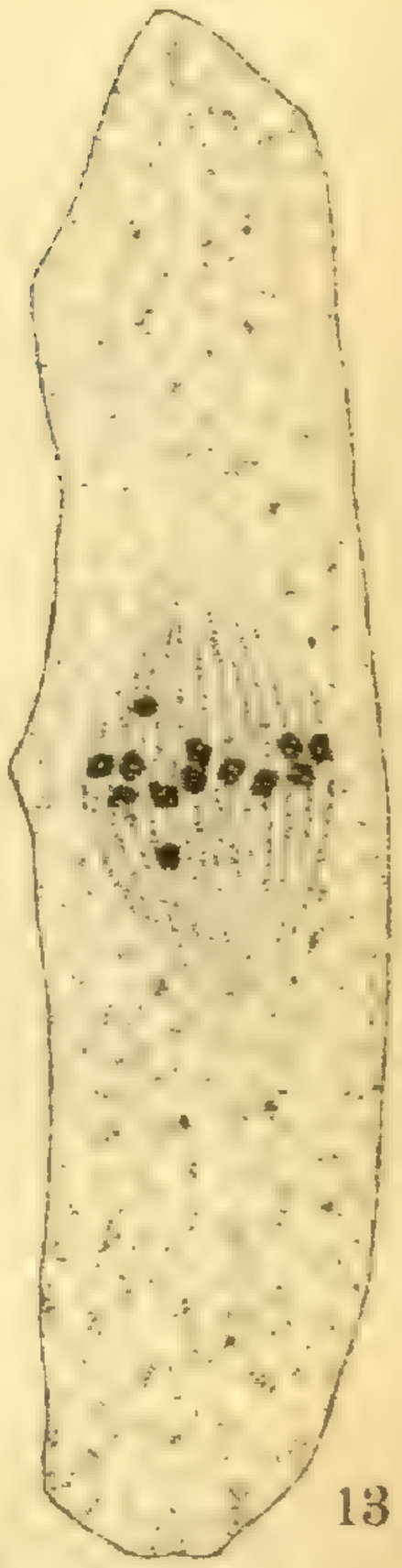

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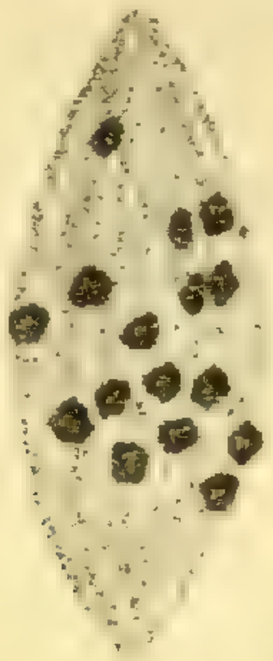

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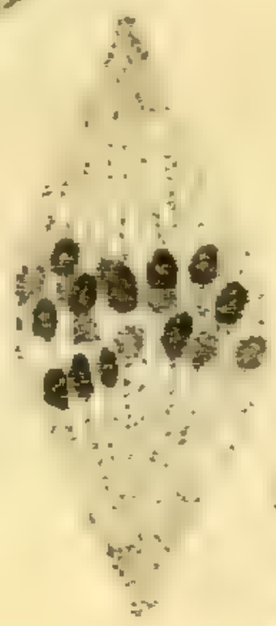

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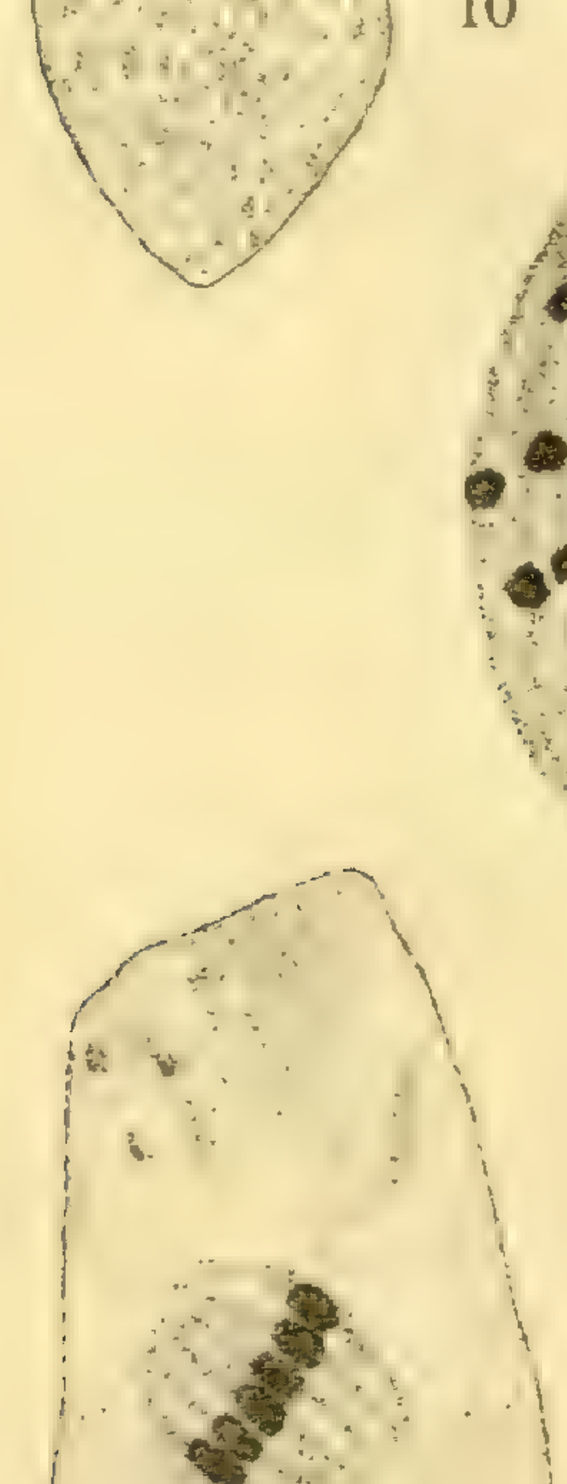

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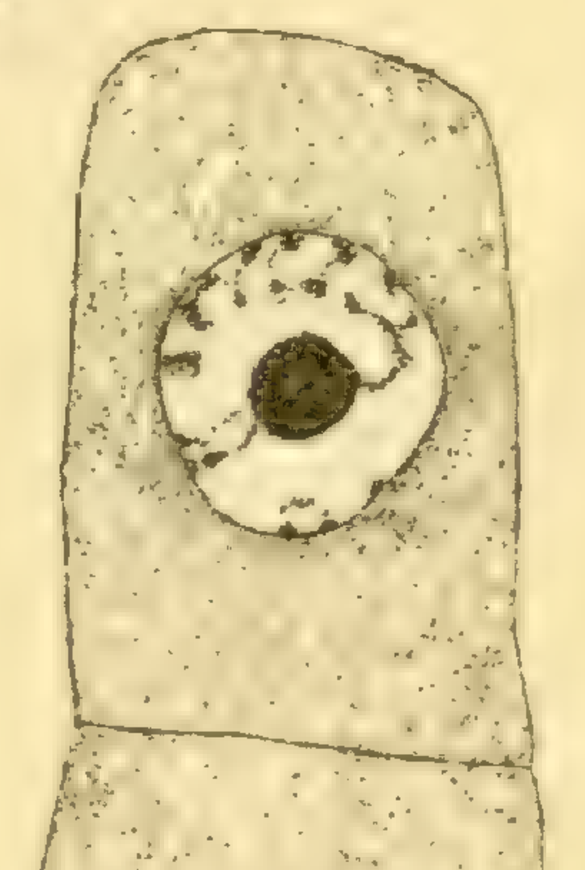

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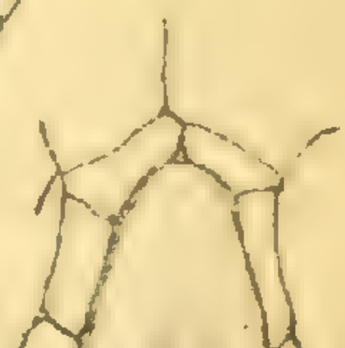

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Microsporogenesis in Datura Stramonium

CLAUDE E. O'NEAL

(WITH PLATES 8 AND 9)

It has long been known that the representatives of the genus *Datura* furnish interesting material easily available for plant experimentation. In addition, it has been pointed out recently (Blakeslee & Avery **2**, **3**) that this genus also affords an excellent field for the study of Mendelian inheritance and mutative variation. The general morphology of the members of the genus is a point of common knowledge, but so far as the writer is aware, no careful cytological studies have been made upon the reduction divisions of any of its members. Guignard (**7**) in his now classical work treats of double fecundation in *D. laevis*. Bönicke (**4**) has examined the prophases and counted the chromosomes in *D. Stramonium*. Aside from these two investigations, the work that has been done upon *Datura* has been of a pharmaceutical or of an experimental character.

The abundance of specimens of *D. Stramonium* near at hand during the summer of 1915 led the author to prepare a large number of anthers for a study of microsporogenesis in this plant. The material was killed, fixed, and embedded in paraffin, in which condition it was kept until the summer of 1919, when an increased interest in the plant as a teaching type induced the belief that a completion of the work and a publication of the results would be of interest. Accordingly, during the months of June and July,

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additional material was secured and the study of the problem renewed.

Material.—The 1915 collection was made from the purple-colored, spiny-fruited plants found growing in an abandoned barnyard near Delaware, Ohio; that collected in 1919 came from plants growing on the Indiana University campus and in a neighboring garden. The plants from both of the latter places were from seed furnished by A. F. Blakeslee. Those in the garden plot were known to be homozygous for the dominant characters, purple color and spiny fruit. The plants on the campus had come about through a series of rather indiscriminate crosses between the purple, spiny-fruited type and the green, smooth-fruited plants described by Blakeslee (2). In making collections from this plot care was taken to select flowers from plants showing the two dominant characters, but since the ancestry was not definitely known, some anthers used may have been taken from heterozygous plants. A careful consideration of the stained cells from the three sources failed to show any appreciable distinction and no attempt was made to keep the preparations separate, but most of the work was done with the Blakeslee strain.

Method.—Parts of the corollas bearing stamens with anthers in various stages of development were killed in the chromo-osmo-acetic and chromo-acetic solutions, washed, dehydrated, embedded in paraffin, and cut into sections 3–5 μ thick. The killing fluid containing osmium gave uniformly better fixation and, in the latter part of the work, its use was adhered to strictly. Haidenhain's haematoxylin and the modified triple stain were used. The orange G of the latter combination was used in clove oil as recommended by Chamberlain and others.

Adaptability of material.—The pollen mother cells of *Datura* offer fair conditions for cytological investigation. Since the anthers in a bud mature their pollen simultaneously, it is necessary to examine a large number to secure the various stages. Some difficulty is attached to the removal of the young cells for the preliminary examination. This probably explains why they have not been examined cytologically before. The sporogenous cells are rather small and have very dense cytoplasm, but the chromatin material is fairly abundant for a dicotyledonous plant. Com-

paratively few chromosomes are formed and the cells stain readily with the usual laboratory dyes.

Anthers.—When the sporogenous cells are developing, the anthers range from two to four millimeters in length; those six millimeters long almost invariably contain mature pollen. Each anther has four loculi, the walls of which are composed of four layers of flat cells. As the anthers mature the cell walls of the two middle layers of these cells become thickened in the fashion usual for mechanical tissue and finally aid in the liberation of the pollen grains. The fourth layer becomes modified to form the tapetum which immediately surrounds the sporogenous cells.

Tapetal cells.—The cells of the tapetum are about the same size as the pollen mother cells when the latter are in the resting condition. At this time they are uninucleate, but by the time the mother cells have reached the spirem stage, they usually contain two or more nuclei, which have arisen from the original one by fragmentation. The tapetal cells increase in size as the spore-producing tissue develops, sometimes attaining a diameter two or three times that of the sporogenous cells. During this development the cytoplasm of most of the cells becomes decidedly vacuolated and, as it continues, the majority of the cell walls break down, and the cell contents are allowed to escape into the pollen cavity. Some of the cells apparently become reduced in size without any evident breaking of the walls, and still others seemingly persist unchanged until the pollen is matured.

The periplasm was carefully searched for "wandering cells" such as were found by Duggar (6) in *Symplocarpus* and more recently in *Galium* by Juel (8), but no positive evidence of such was found. Occasional cells were observed which had apparently broken loose from the anther wall. These were always angular in outline and were attributed to faulty manipulation rather than to any evidence of vital phenomena. Tapetal nuclei are not abundant in the periplasm; sometimes they may be seen as elongate, irregularly shaped structures, similar to those described by Pickett (13) for *Arisaema*, but more frequently as mere darkly staining fragments. No amoeboid forms were found.

Sporogenous cells.—The pollen mother cells arise directly from the primary sporogenous cells without division (Coulter & Cham-

berlain, 5); this accounts for their comparatively small number. In the resting stage they are about 25 μ in diameter and have large prominent nuclei. The cytoplasm is very dense and in the stained preparations seems to be composed of minute particles closely placed. As development proceeds these particles become more or less clumped and arranged in strands as shown in the figures. No evidence of mitochondria or other extra-nuclear bodies was found, but it is not doubted that such might be revealed if proper fixing and staining methods were used.

Nucleus.—In the so-called resting stage the nucleus has a diameter about two thirds that of the containing cell. It usually has a single darkly staining nucleolus, but occasionally two are found. The linin reticulum is composed of very delicate fibers upon which the chromatin material is arranged in the form of minute bodies (FIG. 1). In the preparations the threads are sometimes broken or else do not take the stain properly, but there seems to be no regular arrangement of either the threads or the chromatin bodies upon them. The material collected was too far advanced to show the telophase of the preceding division, but to all appearances the chromosomes of this phase lose their individuality in the maze of fibers and very small and numerous granules seen in the resting stage. It would seem impossible to trace a definite set of these fibers and chromatin masses to a particular chromosome, as Nothnagel (11) was able to do in the case of *Allium*.

FROM RESTING STAGE TO SPIREM

The synaptic condition is reached while the anthers are still quite young (FIG. 4). The initiation of this stage is marked by a thickening and consequent contraction of the linin threads (FIG. 2), which when continued results in their withdrawal from the periphery of the nucleus as shown in FIG. 3. Before the thickening has proceeded far the threads stain readily and their ramifications may be made out easily. The stage represented by FIG. 2 was studied carefully for evidence of the two spirem threads reported by Bönicke (4) for this plant. It will be noticed that the threads apparently anastomose freely and occasionally approximate as shown in the middle of the figure. Whether or not the two ap-

proximating threads occasionally seen should be considered spirem threads in the sense that Bönicke uses the term the writer is unable to determine. This approximation cannot be observed in every cell in this stage of development; it is more in evidence in the figure than is ordinarily seen. In other parts of the same nucleus the threads seem to radiate from chromatin masses, and in still other places the threads seem to be formed by the union of three or more smaller ones. To the mind of the writer the effect is so confusing, that he feels that anyone with a bias in his thinking, no matter what it might be, could find an apparent basis for it here. FIG. 3 shows a stage a little later than that shown in FIG. 2. The linin-chromatin mass has withdrawn from the nuclear membrane and is enveloping the nucleolus. In case two nucleoli are present one of them may be left out of the synaptic ball. At this time the threads and chromatin masses have increased greatly in thickness and stain sharply. On account of the contracted condition the arrangement can not be made out so readily as in the stage just preceding.

Synapsis.—This term is used in botanical literature for the condition shown in FIG. 4. The nucleolus is closely enveloped in the chromatin mass, but its outline as well as that of the threads may be distinguished. The details of the threads, however, can not be made out even in the most carefully stained preparations. This stage occurs so regularly and the sequence is so evident that it is hard to believe that it is an artifact, as Schaffner (14) asserts for *Agave*. In it the formation of the spirem thread is consummated.

Hollow spirem.—FIG. 5 shows the spirem thread as it emerges from the synaptic ball. At this time it is rather thin and when stained with suitable density it appears granular in nature. If the stain is dense, it appears as a fairly smooth thread without any internal differentiation whatever. At this stage no evidence of the double nature of the thread could be made out. Later the thread becomes more loosely arranged in the nuclear cavity as shown in FIG. 6. So far as it has been possible to determine, it is endless.

FORMATION OF BIVALENTS; METAPHASE; ANAPHASE; TELOPHASE

The stage represented in FIG. 6 is followed by a contraction and consequent thickening of the strand. The slightly thickened

strand has a tendency to become arranged in loose loops, which are cut off to form bivalents. In this behavior *Datura* is strikingly similar to *Lilium* as described by Mottier (9). FIG. 7 represents an early segmentation stage. It may be observed from this figure that all of the bivalents are not formed by the cutting off of loops from the spirem thread but that some of them must arise from the straight loopless part of it. Shortly before the segmentation of the chromosomes is brought about, the double nature of the thread becomes evident for the first time (FIG. 11). When segmentation is complete the twelve bivalent chromosomes may be made out. These bivalents may assume a number of different shapes as shown in FIGS. 9 and 10. Some of them appear as closed rings, others as U's, and still others have the chromosomes twisted about each other. The method of forming these various types is easily seen. The loops cut off from the spirem (FIG. 7) form the rings by the union or overlapping of their ends. If the ends are not united or overlapped the U-shaped form results, while the twisted form of bivalent results from the contraction of a loop with a twist in it. Payne (12) has shown that in the European earwig ring-shaped chromosomes may arise in three different ways in the same individual or even in the same cell. So far as it has been possible to determine, the method given above is the only one followed in *Datura*. In *Agave* (14) Schaffner was able to find a constant number of the various types of chromosomes present. A careful consideration of the cells of *Datura* fails to show any regularity in this respect.

Preceding the metaphase the bivalents appear in the multipolar arrangement so often described. This stage is of very short duration and difficulty is experienced in securing it. In the second division it is much more evident (FIGS. 16, 17). In the metaphase the bivalents become arranged in the usual fashion in the middle of the cell. In a polar view they are seen to have a regular distribution (FIG. 13). In this stage the chromosomes appear more or less heart shaped when viewed from the side (FIG. 12) and closely resemble Mottier's figure for *Helleborus* (10). There is no separation of the two halves of the chromosomes on the way to the poles, although the longitudinal division has doubtless taken place (FIG. 11). FIG. 14 shows a telophase stage with the chromosomes

still undivided. The volume of the chromatin material is considerably reduced between the segmentation of the chromosomes and their separation in the anaphase (FIGS. 6, 7, 8, 9, 11). As usual in the dicotyledonous plants a cell wall is not laid down till after the second division (FIG. 18).

SECOND DIVISION; MICROSPORES; POLLEN GRAINS

The material from which this study was made was taken from plants that were growing rapidly, and in it the chromosomes do not become diffused nor in any way lose their individuality between the first and second divisions. It sometimes happens that they become arranged to form a sort of a broken spirem, but each individual may be made out in it easily. This does not seem to occur with any regularity and the relation established is an approximation rather than a fusion of material. Whether or not the chromosomes behave any differently when growth is less rapid has not been determined. FIG. 15 shows a stage slightly further advanced than that represented by FIG. 14. Here the double nature of the chromosomes due to longitudinal splitting or separation is very evident. The next step in the process is a breaking down of the nuclear membrane and the formation of a typical multipolar spindle. When this multipolar condition first appears the chromosomes are seen to be more or less clumped in the midst of the weft of fibers. At this time (FIG. 16) the double nature of the chromosomes is somewhat obscured, but soon they become separated somewhat and their true nature may be made out easily (FIG. 17). In the bipolar spindle which soon follows, the chromosomes are arranged in a very exact fashion, giving the cell an almost diagrammatic appearance. In the following anaphase each chromosome is parted longitudinally and the halves started towards opposite poles. Following the telophase of this division (FIG. 18) a nuclear membrane is formed and the substance of the chromosomes again becomes arranged in the form of a reticulum similar to that seen in the resting condition of the mother cell. The material at hand does not show the details of this process. The walls separating the four cells appear about the time that the nuclear reticulum is established. The cells of the tetrads thus formed cling together for some time before separating as microspores. Shortly after

their separation the nucleus of each divides to form the generative and tube nuclei. Meanwhile the cell has increased in size greatly and a large central vacuole has been formed. A plasma membrane is formed about a portion of the cytoplasm containing the generative nucleus, thus forming the generative cell and completing the development of the pollen grain.

DISCUSSION

It is felt that anyone giving a cytological paper on a field so well-worn as that of the reduction divisions should have a distinct purpose in so doing. It is evident that such work can not reveal much that is strikingly new. A consideration of the literature of plant cytology shows that while many plants have been investigated few of the results have been correlated with the results of experimental work. Many of the plants studied cytologically have been monocotyledonous and not readily amenable to Mendelian investigation. Blakeslee (2) has shown that *Datura* has at least two pairs of characters that show Mendelian behavior with almost mathematical exactness. Such a result must be due to a precise handling of the hereditary substance and to the selection of unmistakeable characters by the plant breeder. The present work shows that there is a very definite apportionment of the chromatin material in the reduction divisions of *Datura*. After the chromosomes are cut off from the the spirem thread they may be traced as distinct individuals till the telophase of the second division. It is evident that, if the factors representing the parental characters are segregated in the two halves of the spirem thread, they would become equally distributed in the formation of the four microspores.

It has long been known that in the insects certain definite characters like sex may be traced to a specific chromosome or part of a chromosome in the reproductive cells. Recently Allen (1) has reported that a similar basis for sex may be made out in *Sphaerocarpos*, one of the liverworts. To one who has studied the cells of *Datura* it is clear that there is no visible evidence of such a basis for the Mendelian characters with which Blakeslee and Avery worked. The determinants of these characters must be chromosomes or parts of chromosomes that are for the present

indistinguishable. In this study no irregularity of chromatin behavior has been found that could explain the origin of mutants, but this could scarcely be expected since their occurrence is comparatively rare. It is conceivable that such might result from the distribution of the chromatin substance in megasporogenesis. If such is the case, it must for the present remain a closed book on account of technical difficulties and the laboriousness of the investigation.

The most striking thing about the chromosomes of *Datura* is their uniformity of size. This is especially evident in the second division. In the first division this uniformity is somewhat obscured by the shapes assumed by the bivalents until they appear in the metaphase.

Interpretation of the prophase.—The behavior of the chromatin material in the formation of the spirem thread has been a much mooted question and it seems that the present study of *Datura* can not shed much light upon it. In the resting condition the nucleus presents such a maze of threads and granules that almost any interpretation might be given. Bönicke (4) claims that the spirem thread is formed by the union of two smaller threads. The writer came to the present problem with a similar theory. As shown elsewhere the confirmatory evidence is not wholly convincing.

No satisfactory theory has been formulated as to how the chromosomes control growth or impart the parental characters to the offspring. It was purposed to make a comparative study of the chromosomes of plants showing the dominant characters and of the chromosomes from plants displaying the recessive characters. Since the rate of growth in the two types is quite different it was conceived that there might be a physical, determinable basis for it in the chromatin substance of the cells. Through an unfortunate misunderstanding the plants showing the recessive characters were destroyed before material was collected for study. Seeds have been planted, however, and it is hoped that work on this phase of the problem may be begun soon.

SUMMARY

1. As a dicotyledonous plant *Datura Stramonium* is favorable for cytological investigation as well as for studies of Mendelian behavior.

2. Part of the bivalent chromosomes are cut from the spirem thread as loops, which if twisted, result when shortened in the twisted form shown in the figures; if the ends overlap, or unite, the ring-shaped form is developed; the U-shaped type may arise from a loop or by the subsequent bending of the straight part of the thread.

3. The report of twelve bivalents made by Bönicke is confirmed.

4. There is no loss of the individuality of the chromosomes from the time that they are cut from the spirem thread till the telophase of the second division. This is an unusually striking phenomenon in *Datura*.

5. The exact results obtained by plant breeders from this plant are attributed to the unusual regularity in the formation and behavior of the chromosomes.

6. No physical basis for the Mendelian characters considered can be found in the chromosomes; nor is any cause found for the occurrence of mutants.

In conclusion, the writer wishes to take the opportunity of expressing his very great obligation to Professor D. M. Mottier, of Indiana University, under whose direction this work was brought to completion, for encouragement and valuable aid given; and to the board of trustees of the Ohio Wesleyan University for a relief from teaching duties that has made possible the pursuance of this investigation.

INDIANA UNIVERSITY

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Explanation of plates 8 and 9

All figures × 2270.

FIG. 1. A pollen-mother cell in resting condition.
FIG. 2. An early presynapsis stage.
FIG. 3. A stage a little later than that shown in FIG. 2.
FIG. 4. Synapsis.
FIG. 5. Coming out of synapsis.
FIG. 6. An early hollow spirem stage.
FIG. 7. Segmentation in process showing method of cutting off the bivalents.
FIG. 8. A stage a little later than that shown in FIG. 7.
FIG. 9. Segmentation.
FIG. 10. Some of the shapes assumed by the bivalents.
FIG. 11. A spirem stage in which the double nature of the thread is shown.
FIG. 12. A bipolar spindle, passing into anaphase.
FIG. 13. A metaphase, polar view, showing the twelve bivalents.
FIG. 14. A telophase.
FIG. 15. A little later stage, in which the double nature of the chromosomes is shown.
FIG. 16. An early multipolar spindle of the second division, showing the clumping of the chromosomes.
FIG. 17. A stage a little later than that shown in FIG. 16.
FIG. 18. Telophases of the second division.

The refraction of light in plant tissues*

FOREST B. H. BROWN

(WITH FOUR TEXT FIGURES)

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I. INTRODUCTION

The laws of refraction have an interest in microscopy, not merely in connection with the definition of anatomical details, but also in the determination of the chemical or physical qualities of any part or product of the cell. Such laws are of universal application, have the advantage of great precision, and serve to differentiate many characters not readily brought out by stains or chemical reagents. Furthermore, a knowledge of the refractive properties of the various tissues is indispensable if one is to obtain the clearest definition of tissue outlines by aid of the microscope. Current methods, however, go little further than listing the indices of refraction of media in which tissues may be mounted,

* Contribution from the Osborn Botanical Laboratory.

all of which have little significance in anatomical work unless the index of refraction of the tissue substances is also given. In as much as many, if not most, of the ultra-microscopic characters of cell membranes are to a greater or less extent associated with the refractive powers of these membranes, the laws of refraction have their special application in the investigation of the physical or chemical composition as well as in the anatomical characters of cell membranes. Such laws, therefore, in their application to plant tissues, come well within the scope of botanical research, and, as such, open a wide field for investigation, particularly when more than ordinary precision is required.

Owing, apparently, to chemical change, the refraction of a plant membrane is peculiarly liable to actual variation during growth; still more characteristic of the plant membrane, due to its hygroscopic qualities, are the apparent fluctuations (deviations) in refraction by virtue of which it absorbs (imbibes) water and other refractive liquids in which it may be immersed.

A study of the refraction of light in plant tissues and of some of the conditions affecting or apparently affecting its stability was carried on by the writer at intervals during the years 1917–1919, at the Osborn Botanical Laboratory. The writer expresses indebtedness to Professor A. W. Evans and other members of the Department of Botany and to the members of the School of Forestry, for every encouragement throughout the investigation; also, to Professor C. S. Hastings of the Department of Physics for many valuable suggestions, and for verification of the work with refractive liquids. The methods described constitute a supplement to the more general technique for woody tissues given in an earlier paper ('19, p. 138).

II. METHODS OF MEASURING REFRACTION WITH THE MICROSCOPE

The methods by which it is possible to determine the refraction of an object (under the microscope) depend on the use of mounting media of known refractive powers. With a gradient series of such media, the index of refraction of an object may be measured with accuracy to the second decimal place.

1. REFRACTIVE LIQUIDS

To measure the refraction of an object microscopically a gradient series of refractive liquids must first be prepared. For plant tissues in the dry condition, a series of twenty liquids differing from each other in refraction by about .005 and ranging from 1.499 to 1.598 was found generally satisfactory. Either aqueous solutions or oils may be used in making up such a series, both water and oil possessing certain advantages over the alternative solvent. Aqueous solutions, for instance, would probably be best for measuring the refractive powers of the living contents of a cell. But such solutions are absorbed by many tissues more than are oils. One in particular of the solutions, to be described presently, the McLean solution, causes great swelling of mucilaginous membranes, which, for certain purposes, is desirable; but unfortunately, it breaks down the structure of starch grains. Water solutions are open to the objection that they tend to evaporate, with the result that the concentration and refraction of the liquids are changed. For general purposes, therefore, non-volatile oil mixtures proved to be superior to aqueous solutions, and a series made up from mixtures of castor oil (n = 1.49) and clove oil (n = 1.535) for refractions below 1.535, and of clove oil and naphthalene α monobromated (n = 1.65) for the higher refractions gave excellent results (n indicating index of refraction). The mixtures and their respective indices of refraction are indicated in TABLE I.

A gradient series of refractive liquids may be prepared by mixing a liquid of high refraction with one of low refraction. When castor oil is mixed with clove oil, or clove oil with naphthalene α monobromated, the index of refraction of the mixture is proportional to the volumes of the liquids mixed. Or, if V_a and V_b are the volumes of the liquids mixed and n_a and n_b the respective indices of refraction, then

$$\frac{V_a(n_a - 1) + V_b(n_b - 1)}{V_a + V_b} = n - 1$$

If a series of mixtures is now prepared, in each of which mixtures the relative volume of one of the oils of known refraction is decreased by a constant quantity (e.g., 10, 9, 8, . . . 0) while the

TABLE I

A SERIES OF REFRACTIVE OILS USED IN THE DETERMINATION OF RELATIVE REFRACTION

The test liquids are made from mixtures of naphthalene α monobromated (naphth.) clove oil (clove), and castor oil (cast.), and are arranged in sequence according to refraction. O indicates in what media the outlines are invisible or nearly so; + or −, that the refraction is either more or less than that of the liquid.

Test liquids			Lignified and furfurol-reacting tissues						Pectin, cellulose tissues						Cell contents		
Vol.		Index of refraction	Pith, *Tilia*	Vessels, *Tilia*	Normal fibers, *Alphitonia* (secondary wall)	Mucilaginous fibers, *Alphitonia*		Bast fibers, *Tilia* (secondary wall)	Middle lamella, *Tilia* (primary wall)	Cambium, middle lamella, *Tilia*	Phloem (soft bast), *Tilia*	Collenchyma *Tilia* = R. membrane, *Pyrus*	Primary cortex, *Tilia*	Reserve cellulose, date seed	Starch, wheat	Aleurone, *Zea*	Calcium oxalate trihydrate	Cork, cuticle
Naphth.	Clove					Secondary layer	Mucilaginous layer											
11	9	1.598	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
10	10	1.592	−	−	−	−	−	−	O	−	−	−	−	−	−	−	−	−
9	11	1.587	−	−	−	−	−	−	O	−	−	−	−	−	−	−	−	−
8	12	1.581	−	−	−	−	−	−	+	−	−	−	−	−	−	O	−	−
7	13	1.575	−	−	−	−	−	−	+	−	−	−	−	−	−	O	−	−
6	14	1.569	−	−	−	−	−	−	+	−	−	−	−	−	−	O	−	−
5	15	1.564	−	−	−	−	−	−	+	−	−	−	−	−	−	O	−	−
4	16	1.558	−	−	−	−	O	−	+	−	−	O	−	−	−	O	−	−
3	17	1.552	−	O	O	−	O	−	+	−	−	O	O	−	−	+	+	−
2	18	1.545	−	O	O	−	O	−	+	O	O	O	O	−	−	+	+	−
1	19	1.540	−	O	O	−	O	−	+	O	O	O	O	O	O	+	+	−
0	10	1.535	O	O	O	O	O	−	+	O	O	O	O	O	O	+	+	−
Cast.																		
1	9	1.531	O	O	+	O	O	−	+	O	O	O	O	O	O	+	+	O
2	8	1.526	O	O	+	O	O	−	+	+	O	O	O	O	O	+	+	O
3	7	1.521	O	+	+	+	O	O	+	+	+	O	O	+	O	+	+	O
4	6	1.517	+	+	+	+	O	O	+	+	+	O	O	+	O	+	+	+
5	5	1.512	+	+	+	+	O	O	+	+	+	O	O	+	+	+	+	+
6	4	1.508	+	+	+	+	O	+	+	+	+	O	O	+	+	+	+	+
7	3	1.503	+	+	+	+	+	+	+	+	+	O	O	+	+	+	+	+
8	2	1.499	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

second is correspondingly increased (0, 1, 2, . . . 10), or in such a way that the ratio of volumes of the two liquids (in a series of eleven mixtures) would be to each other in the successive mixtures as $\frac{10}{0}$ $\frac{9}{1}$ $\frac{8}{2}$ $\frac{7}{3}$ . . . $\frac{0}{10}$, then the indices of refraction of the respective mixtures will form a gradient series (see TABLE I). In order to obtain any required difference in refraction between consecutive liquids in the series, it is only necessary to determine the constant by which the relative volumes are consecutively changed.

To measure the volumes, a medicine dropper may be used, but allowance must be made for the relative size of a drop in each

case. This may be done by measuring at room temperature (70° F.) the volume of 200 drops of each of the oils used in the mixture. By this means a drop of castor oil was found to have a volume equal to that of 1.8 drops of clove oil, and 1 drop of naphthalene α monobromated, 0.95 the volume of a drop of clove oil.

2. PREPARATION OF THE TISSUES FOR STUDY

In preparing tissues for the measurment of their refraction the following schedule was adopted.

1. Cut as many sections, 10–40 μ thick, as there are refractive liquids in the series, and wash in water for 10 minutes or longer.

2. Transfer each section to a separate slide and cover with a glass slip.

3. Dry for at least fifteen minutes at 100° C. An electric oven is useful for this purpose.

4. Remove the slides one at a time from the oven and mount each section in a different refractive liquid of the series. The samples of tissue are then ready for microscopic examination.

3. DETERMINATION OF RELATIVE REFRACTION

For this purpose, an apochromatic microscope with Abbé condenser and movable sub-stage diaphragm was used, but any microscope with the usual accessories will answer for ordinary purposes. A magnification of about 800 diameters was usually used in the examination. The refraction of the object relative to that of the liquid was determined in each case by one or more of the following methods.

A. By oblique illumination

The partly-closed sub-stage diaphragm is shifted to one side. If the refraction of the tissue mass is above that of the liquid, the outlines appear dark on the side toward which the diaphragm is shifted. But if the refraction of the tissue mass is below that of the liquid, the outlines appear dark on the side away from which the diaphragm is shifted. In TABLE I the refraction of the tissue or body examined is indicated as + (above) or − (below) with respect to the refractive index of the liquid in which it is immersed.

If the dispersion (i.e., the difference between the indices of refraction of light of long and of short wave-length) of the liquid is not the same as that of the object, it is possible to find a common index of refraction for light of one wave-length only. In this case, the refracted rays give fringes of color such as blue on one side and red on the other. McLean's solution, which has a high dispersion, causes wide color fringes with the reserve cellulose of date seed, in dilutions having a refraction between 1.531 and 1.535. This method is particularly useful in determining whether the refraction of an object is above or below that of the liquid.

B. By direct illumination

Relative brightness.—In studying tissues, the relative refraction of a transparent object is often indicated by the illumination of its transverse surface. On raising the tube of the microscope slightly from sharp focus, an object whose refractive index is higher than that of the tissues or liquid in contact with it appears relatively bright except at the border (see FIGS. 1 and 2). An object of lower refraction, on the other hand, appears relatively dark. On lowering the tube the relative brightness is reversed in each case.

The Becke line.—A few bodies, such as the crystals of calcium oxalate in the crystal-parenchyma of woody tissues, are visible in all liquids of the series. The refraction of such bodies is best determined as follows: An uncovered edge of the crystal is found, which projects into the liquid. When brought into sharp focus, a narrow band of bright light—the Becke line—defines the outline. On focusing upward, this band of light appears to move in the direction of the body of highest refraction, i.e., outward from the border into the liquid, if the refraction of the liquid is higher than that of the crystal, or inward from the border toward the centre of the crystal if the refraction of the crystal is higher than that of the liquid.

C. Modifications with hygroscopic tissues

In applying the methods above described to plant tissues, certain modifications are necessary, due to the fact that most membranes tend to imbibe the refractive liquids in which

they are immersed and to become invisible in two or more liquids of the series. This latter phenomenon is attributable to the fact that the refraction index of the mass, i.e., the dry tissue substance together with whatever of the refractive liquid may have been imbibed, here approaches that of the liquid in which it is mounted; and under these conditions it would be recorded as O in the tabulation (see TABLE I). In such cases the refractive power of the tissue substance is taken as the mean between the liquid of highest refraction and the one of lowest refraction in which the outlines are barely distinguishable. Further observations regarding the refraction of hygroscopic bodies are made below.

D. Relative accuracy of the methods

The accuracy with which the index of refraction of an object may be determined by the foregoing methods obviously depends, in the first place, upon the accuracy of the calculated indices of the liquid mixtures. In a test made of one of the liquid mixtures (castor oil, 5 volumes: clove oil, 5 volumes), for example, all the figures in the calculated index (1.512 +) were found to be correct; in fact, no errors were found in the calculated indices of any of the mixtures; but for extreme accuracy, the index of refraction of the liquid should be standardized as a matter of precaution.

With accurately standardized liquids, the index of refraction of minerals may, according to Wright ('11, p. 96), be determined with an exactness of ±.001 when monochromatic illumination (strong sodium light) is used, and Wright considers the method by oblique illumination about as accurate as the Becke line method. By the Becke line method the refraction of calcium oxalate trihydrate was found by the writer to lie between 1.568 and 1.552; and with a series of liquids intermediate in refraction between the ones used, it would doubtless have been possible to have made a more exact determination. The method employed to determine the refraction of hygroscopic bodies is less exact than methods applicable to crystalline bodies, but determinations may be carried to the hundredths with reasonable accuracy.

III. REFRACTION OF TISSUES

The results recorded in TABLE I bring out wide relative differences in refraction in different tissues or in different parts of

the same tissue; also, it is seen that the index of refraction of any given membrane may deviate widely from the average or may actually change during growth.

1. RELATIVE REFRACTION

As shown in TABLE I, there is no single index of refraction which is common to even the different membranes of a tissue. A fair average for dehydrated tissues would be 1.53, or .01 above that of Canada balsam or dammar (1.52); but the refraction of many bodies, particularly the cell contents, differs widely from the mean. For the dehydrated tissues examined by the writer, n (the index of refraction) varies from 1.50 to 1.59; but had protoplasm and other living bodies with high water content been included, far lower refractions would doubtless have been found, and the range in refraction would probably have been about three times as great.

2. DEVIATION IN REFRACTION WITH IMBIBITION

Certain crystalline bodies found in plant tissues, such as the crystals of calcium oxalate, do not become invisible in any of the refractive liquids: no physical change takes place when they are brought in contact with the oil mixtures and no deviation or change in refraction occurs. An organic membrane on the other hand, as already noted, imbibes the liquid in which it is mounted. As a result of the physical change which thus results in the mass of the membrane, the latter becomes invisible, or nearly so, in two or more consecutive liquids of the refractive series, namely, in those whose index of refraction approaches most closely that of the membrane after it has absorbed as much as it will of the refractive liquid in which it is mounted. In other words, the refraction of the membrane mass, after imbibition, deviates from that of the tissue substance according to the volume and refractive index of liquid taken up, the principle involved being nearly the same as that observed in preparing the series of refractive liquids.

Different membranes show great differences in the relative deviation of refraction. Cuticle, cork, true wood fibers, and middle lamella, for example, show relatively little deviation; collenchyma, primary cortex, and mucilaginous membranes, on the other hand,

take up relatively more of the liquid and show a correspondingly wide deviation in refraction.

The imbibition of liquid is also indicated by the swelling of the membrane, and those membranes which have the widest deviation in refraction, as, for example, the mucilaginous membranes in woody fibers, are the ones which swell the most. Not infrequently such membranes, as shown by an accurate projection published in a previous paper ('19, p. 143), may swell to almost double thickness when dehydrated sections are mounted in water, glycerine, or McLean's solution. But refraction is a more delicate index than swelling in that it serves to differentiate the particular portions of a membrane which take up the liquid.

Some extremely hygroscopic membranes are invisible, or nearly so, in liquids differing in refraction from one another by more than .055. There thus is an apparently close relation between imbibition and refraction. But since visibility of outline is partly dependent upon other factors, such as the relative light dispersion of the liquid and the object, the deviation in refraction may not be exactly proportional to the imbibition of liquid.

3. CHANGE IN REFRACTION WITH GROWTH

Deviations or apparent fluctuations in refraction, such as those above described, are not associated with any actual change in refraction of the membrane substance; on removing the imbibition liquid from the tissue, the refraction of the membrane is found unchanged. But, during growth, actual changes in refraction may occur, as, for example, in the middle lamella of wood cells. In the early stages of cambial growth, such as may be found in the stems of woody angiosperms, the membrane which subsequently becomes the middle lamella has a refractive index of about 1.53, or the average for plant tissues. In subsequent stages, such as occur in the narrow zone of undifferentiated tissue next to the true cambium, where the thin-walled immature cells are in various stages of elongation, the refraction of this membrane increases with progressive differentiation. Thus, as soon as growth in length of the wood cells has ceased and the walls begin to thicken prominently by apposition—the stage in which the first secondary thickenings of the fibers appear and the tissue

hardens—there is a rapid rise in the index of refraction of the middle lamella to 1.59, or .135 above that of glycerine (FIG. 1), at which it remains nearly constant. Such a change in refraction can hardly be explained except in relation to a change in the chemical composition of the pectin lamella, as a result of which, beginning as a membrane of average refraction, it quickly becomes the most refractive of all.

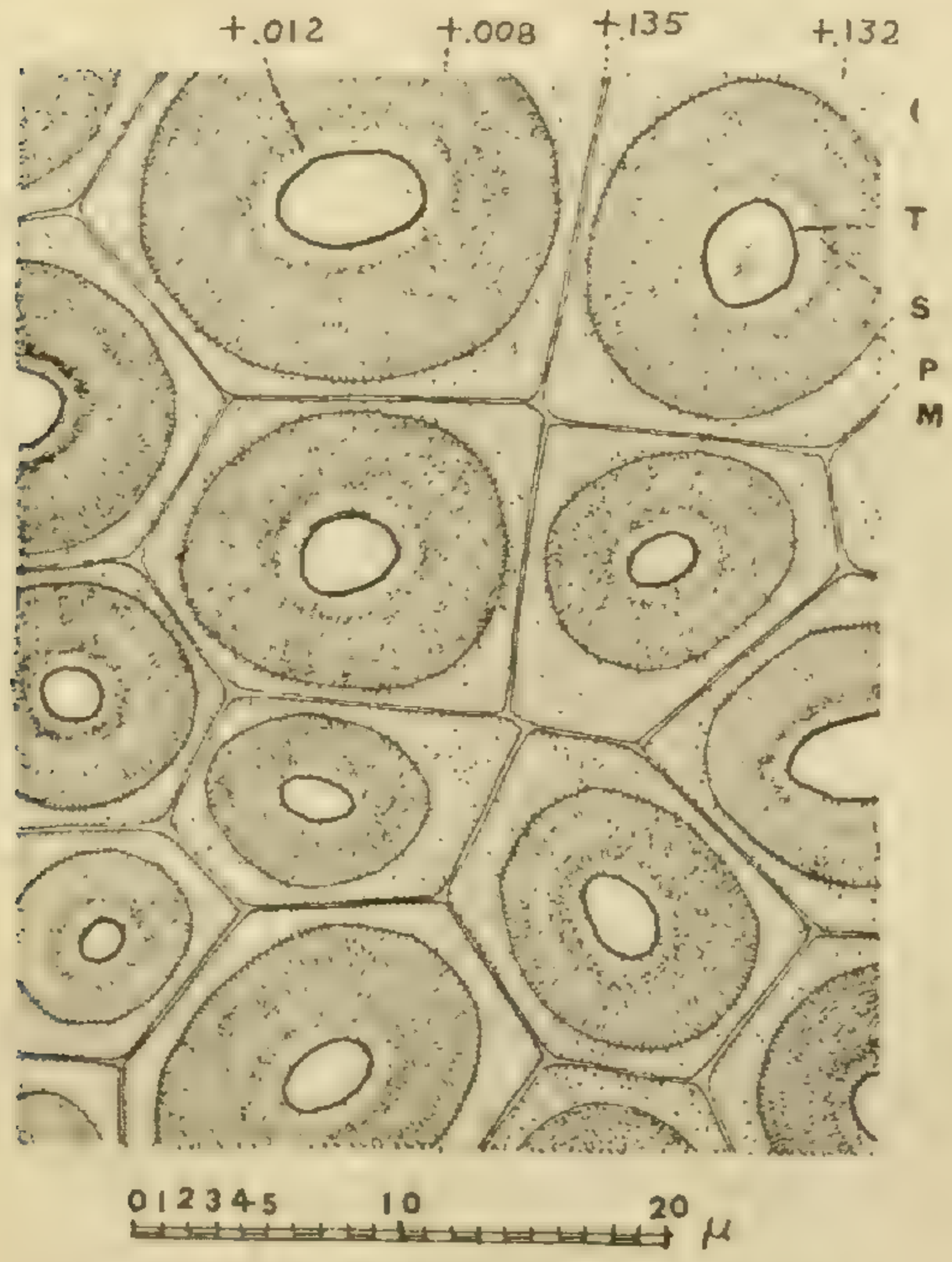

FIG. 1. Abbé camera drawing of fibers of Ipê tabaco (*Tecoma* sp.), mounted in glycerine (n = 1.46). All membranes are + with reference to the glycerine medium. In upper sharp focus, the refractive membranes appear bright; this is indicated in the shading. The middle lamella (M) is less distinct in glycerine than indicated in the drawing. The membranes (M, middle lamella, and P, primary thickening of the fiber) are highly refractive (n = 1.59) and appear brightly illuminated, especially the middle lamella. The secondary layer (S) is less refractive (n = 1.54) and relatively dark. T, tertiary thickening.

The primary thickening of wood fibers (P, FIG. 1) is also composed of a highly refractive material. In xerophytic species of *Tecoma* and a number of other woods, this membrane first appears as a collenchyma-like thickening upon the sides of the middle lamella, in cells which lie near the true cambium, and which have not ceased to elongate and to glide upon one another. This membrane, though much thickened in species of *Tecoma* and certain other genera, is ordinarily thin and, because of similarity in the refractive and staining qualities, is likely to be mistaken as part of a somewhat thickened middle lamella. Both membranes stain deeply with haematoxylin, methylene blue, fuchsin, and other stains for pectic bodies, and together constitute by far the most refractive (.132–.135 above glycerine) membranes in the mature xylem. But the refraction of the primary wall is slightly lower (about .003) than that of the middle lamella, and, when observed in a refractive medium at which the former becomes invisible (about 1.545 for

Tecoma), the true middle lamella is nearly as sharply defined as in collenchyma (C, FIG. 2).

The observed differences in refraction here are probably associated with differences in mineral content of the membrane studied. Of the mineral elements which enter into the composition of woody tissues, calcium, especially in the form of calcium carbonate, would seem to be the only one likely to bring about an increase in refraction as great as that noted in the middle lamella and primary wall. The presence of silica, for example, in portions of the secondary layer (FIG. 1, *S*) is associated with a much lower refractive index.* The rise in refraction of the middle lamella and primary wall during development finds its most reasonable explanation in the supposition that in these pectic membranes the relative proportion of calcium is greatly increased as soon as the cells have attained their mature size and the mechanical tissues begin to acquire hardness and strength. Apparently, these membranes acquire their mechanical rigidity as a result, in part at least, of the addition of calcium, possibly in combined form, to the pectin; and it is of interest to add that both by chemical treatment and by the action of certain enzymes, as will be described presently, the primary wall may be softened and the middle lamella reduced to a jelly-like consistency, so that cells glide upon one another as during development; even closing membranes of

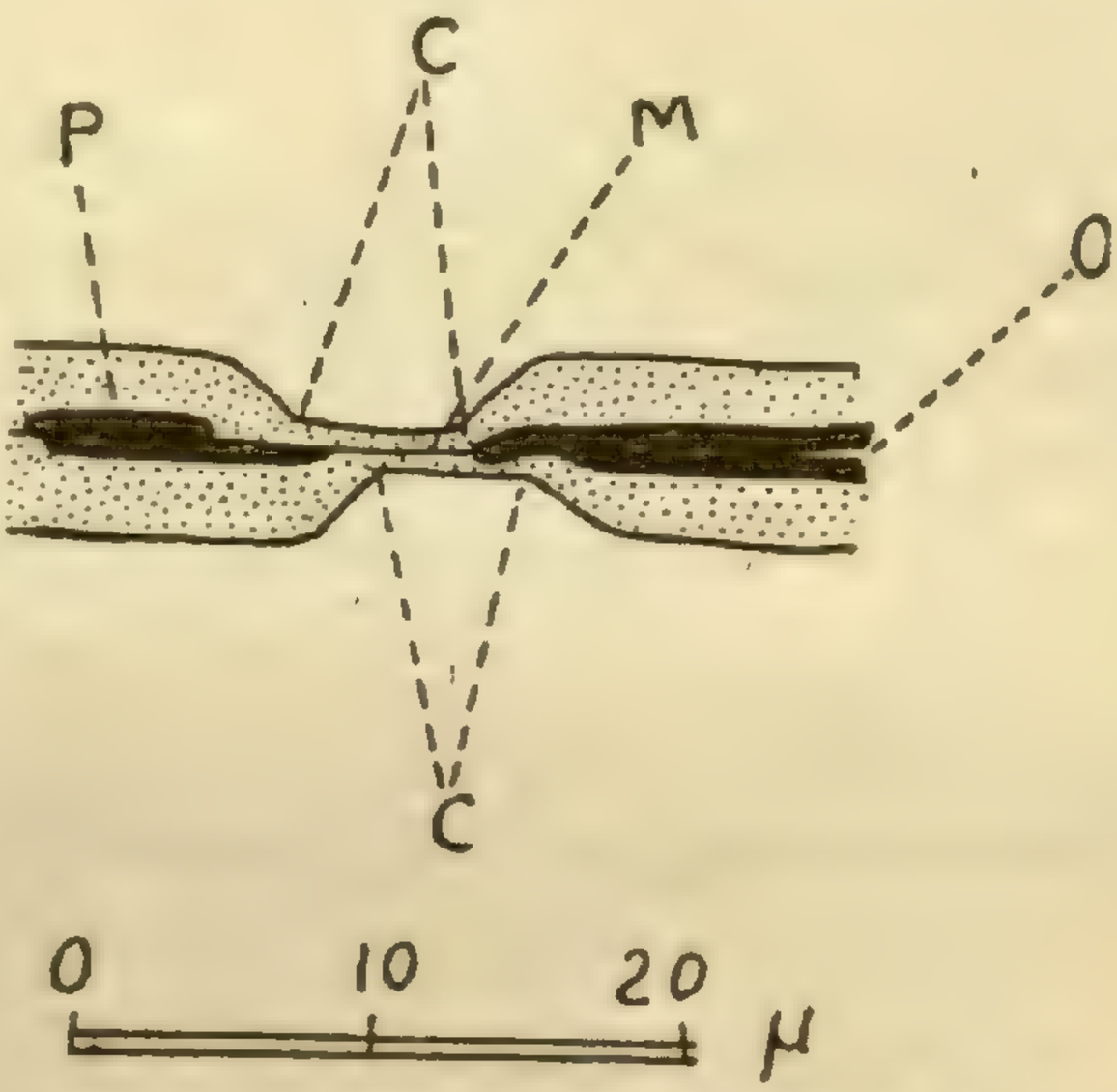

FIG. 2. Longitudinal section of a wall between two thick-walled parenchyma cells in the stem of *Dracaena aurea*, after twenty-four hours treatment in Easter lily pollen enzyme solution. The middle lamella (*M*) has softened, allowing the cells to glide upon another, the closing membrane (*C*) of a simple pit has separated longitudinally along the middle lamella and one part has glided upon the other. In places, the primary wall (*P*) is shown stained deeply with haematoxylin and at *O* it has separated along the middle lamella.

* The presence of highly silicified longitudinal tracts in the secondary layer of wood fibers of *Tecoma* has been demonstrated by the writer and will be published in a subsequent paper on fiber skeletons.

pits may be split in a manner similar to that observed by Neeff in growing fibers of wood ('14, p. 503) and bast ('14, p. 510).

The treatment by which the middle lamella was softened is as follows: thin sections (3 μ thick) of the wood of *Dracaena* were placed for twenty-four hours in a 25 per cent alcoholic solution of hydrochloric acid, then for twelve hours in 20 per cent ammonia. After such treatment the primary wall and particularly the middle lamella were etched and softened to a degree that permitted cells to glide upon one another, the closing membranes of pits were divided along the middle lamella, so that one part moved upon another. By this treatment with acid alcohol, according to Mangin (Haas and Hill, '13, p. 127), the combined pectin is freed from its bases (e.g. calcium) and is then dissolved by the ammonia. It is of interest to note that an effect similar to that obtained by hydrochloric acid and ammonia (FIG. 2) was obtained by placing sections, 2.5 μ thick, for twenty-four hours upon wet Easter lily pollen moistened with water, the membranes, in this case, being acted upon by an enzyme. In sections of *Tecoma*, the middle lamella and primary walls were similarly etched and softened.

Not only the middle lamella and primary wall but also all other tissue elements have, with possibly a few exceptions, a characteristic refractive index; it is remarkable to what an extent the various membranes become differentiated in their refractive properties during growth. As will be shown presently, a membrane which can hardly be differentiated by reagents may be clearly defined by its refractive properties.

IV. DEFINITION OF ANATOMICAL DETAILS

Success in obtaining clear microscopic definition is in no small measure dependent upon the refraction of light by the mounting medium. It is of the utmost importance that the index of refraction of the tissue should bear a definite relation to that of the medium in which it is mounted.

1. REFRACTION OF MOUNTING MEDIA

When the refractive properties of a tissue are known, definite refractive effects may be obtained by selecting media having the necessary indices of refraction. The following list (TABLE II) includes some of the refractive media most useful for this purpose:

TABLE II

REFRACTION OF MEDIA

	Index of refraction
1. Water	1.336
2. Alcohol	1.37
3. Fluorite	1.433
4. Glycerine jelly	1.44
5. Glycerine	1.46–1.47
6. Castor oil	1.49
7. Xylol	1.50
8. Oil of red cedar (*Juniperus procera*)	1.512
9. Crown glass	1.518
10. Dammar; Canada balsam	1.52
11. Clove oil	1.535
12. Quartz	1.544
13. Styrax	1.58
14. McLean's solution; flint glass	1.621
15. Balsam of Tolu	1.628
16. Naphthalene α monobromated	1.65
17. Iceland spar (calcium carbonate) (Hastings '88)	1.658 and 1.48
18. Tolu dissolved in naphthalene α monobromated	1.72
19. Quinidine	1.8?

A few comments on some of the various media listed may be made:

Water; alcohol.—These media have an index of refraction far below (a difference of about −0.20) that of the average for plant tissues. If the section is thin, these media have no superior for the definition of minute details in tissues which shrink on dehydration. But, on the other hand, a section of ordinary thickness (20–70 μ) lacks transparency in these media and the outlines are confused. In such sections, greater transparency and therefore clearer definition may be obtained by mounting in some medium such as xylol, whose index of refraction differs but little (about 0.02) from that of the tissue.

Glycerine; glycerine jelly.—Unstained sections of stem tissues, from which air has been removed by standing in alcohol, mounted in glycerine and permanently cemented with Brunswick black or gold size, require little time to prepare and are frequently superior to stained sections for observing minute details such as the pitting of fibers or vessels, as well as the broader details of outline. Glycerine jelly is particularly to be recommended for unstained sections of woody tissues.

Dammar; Canada balsam.—It is unfortunate that the refractive index of both dammar and Canada balsam approach too closely those of the stem tissues to allow their use for mounting unstained sections of any of the hygroscopic tissues of the stem. Details in some of the soft tissues of the bark, as will be shown presently, are also obscured through shrinkage during the process of dehydration. These media have a refractive index about .01 below the average for dehydrated plant tissues and, for general purposes, are fully deserving of the esteem in which they are held as media for mounting stained sections.

McLean's solution.—This solution, suggested by McLean ('14), is prepared by dissolving in a saturated aqueous solution of potassium iodide as much mercury biniodide as it will take up. This solution has a high index of refraction (1.6210 for solution of full strength), equal to that of flint glass and far exceeding that of any of the tissues examined; it is readily diluted with water, the index of refraction of which is lower than that of any constituent of plant tissue. This liquid may therefore be regarded as one of the best for preparing a series of aqueous dilutions for measuring refraction in tissues, and the principle involved in diluting with water is the same as that earlier given and adopted in mixing the oils of a refraction series. By such a series of liquids a wide range in refraction (1.33–1.62) may be covered, and if successive dilutions were made to differ from each other by $n = .005$, there would be 59 liquids in this series. As before mentioned, tissues imbibe aqueous solutions more readily than the oils, causing wider deviations in refraction, but the mean refractions of tissues determined by their use were the same as those determined by oils. McLean's solution also has high dispersion or, in other words, a wide difference between the index of refraction for light of long wave-length (red) and light of short wave-length (blue).

As a medium for mounting soft tissues, this solution possesses the advantage of not requiring dehydration, so that such tissues may be mounted directly without danger of shrinkage. But it has the serious disadvantage of causing wide deviation of refraction in certain tissues, such as collenchyma, as a result of which the outlines may become quite invisible.

Tolu.—This oleo-resin (balsam), obtained from the bark of a leguminous tree, *Myroxylon toluifera* H. B. K., of South America, brings out satisfactorily the pitting and other details of unstained macerated preparations.

Naphthalene α monobromated.—If sections are thin, naphthalene α monobromated defines clearly all tissues of the stem. Where dehydration can be accomplished without too great shrinkage of the tissue, details such as the pits in hypodermal collenchyma appear very distinctly. This oil is also one of the best for use in measuring refraction of tissues by the microscopic method.

Quinidine.—This is perhaps the most satisfactory medium of all for the definition of minute details. Also, all tissues of the bark appear clear and well defined except for details affected by shrinkage or high temperature. In using this organic substance, it is liquified on the slide at a temperature above that of boiling water. Professor Hastings states that quinidine crystallizes or spoils with time and, further, that highly refractive media, such as quinidine, tolu, and styrax, define with great clearness the minute details of diatom cysts.

2. PITS AND MIDDLE LAMELLA IN COLLENCHYMA

The part played by refraction in bringing out details may be demonstrated by comparing cross-sections of the collenchyma of some woody stem, such as *Pyrus communis* L. or *Aucuba japonica* Thunbg., mounted in Canada balsam with sections mounted in other media. In balsam mounts the prominent system of pits connecting the cells is usually obscured (FIG. 3, *A*), whether stained or not, and it is worthy of note, in this connection, that the presence of such pits in the collenchyma of woody stems, though a characteristic feature of this tissue in nearly all dicotyledonous trees and in many other woody plants, has seldom been noted in anatomical drawings or descriptions, even in such standard texts as that of Moeller ('82), although it can be readily seen when in sections which have been mounted in suitable media (FIG. 3, *B*). Thus, this pitting system becomes very clear in naphthalene α monobromated, invisible or nearly so in potassium iodide-mercury biniodide, and visible again in glycerine (FIG. 3 *B*) or water. The middle lamella, however, is not clearly defined in any of these

media; but if the section is mounted in a medium whose index of refraction (about 1.526) approaches sufficiently close to that of the inner and outer thickenings (*I* and *O*, FIG. 3), then the middle lamella, whose index of refraction is higher (+) than this, stands out plainly (as indicated in FIG. 3, *C*) and is the only portion of the wall which can be seen even under the most favorable conditions of illumination. In alcohol and quinidine, dehydration may cause shrinkage of the tissues to such an extent that not as good results are obtained as would be expected from the refractive

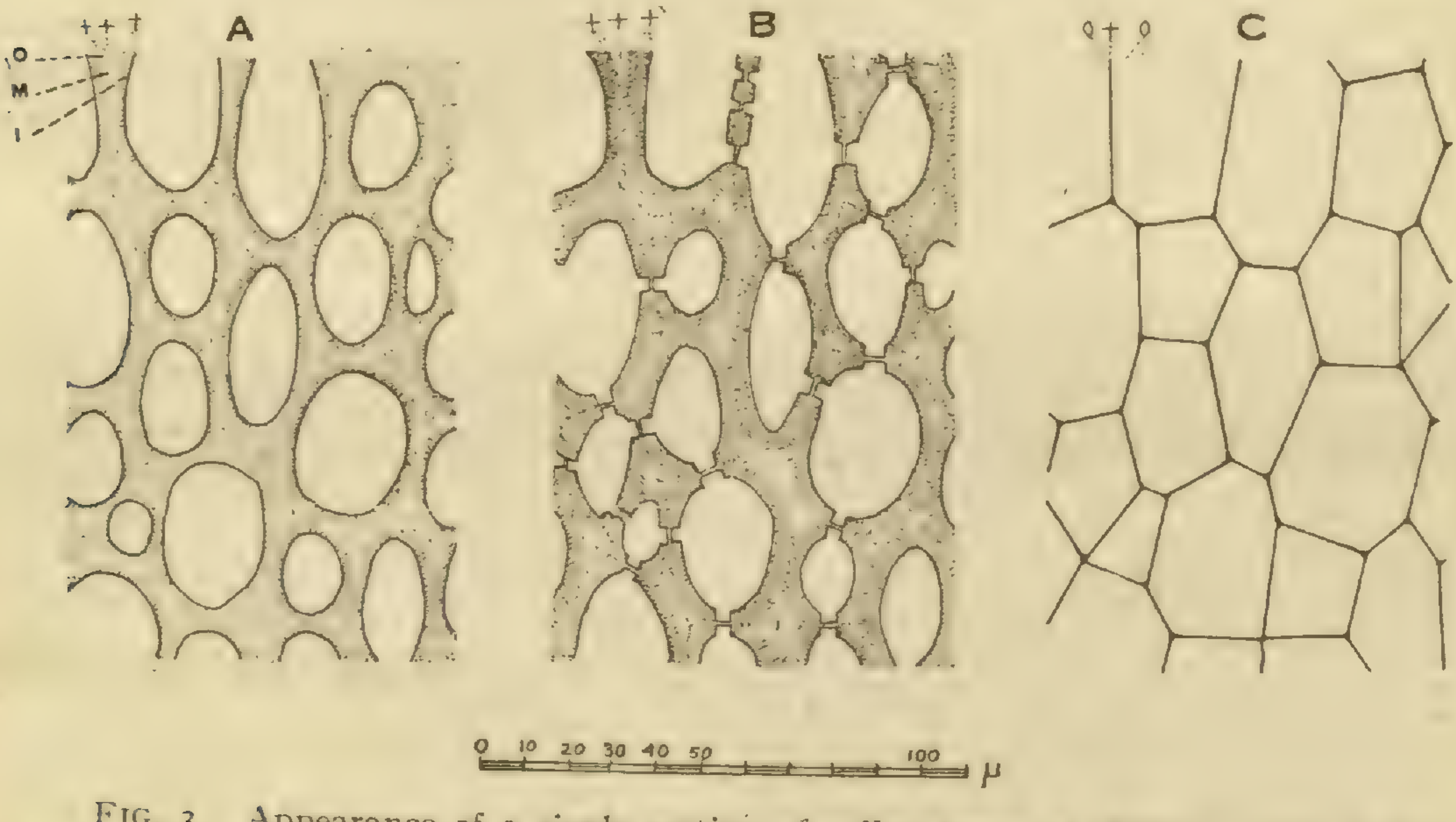

FIG. 3. Appearance of a single section of collenchyma of *Pyrus communis* L. mounted in three different refractive media. *A*, in Canada balsam, $n = 1.52$; there is little or no definition of minute detail. *B*, the same section as *A*, but mounted in glycerine, $n = 1.46$; the pits are clearly defined. *C*, again the same section, but mounted in a mixture of castor oil, 2 volumes and clove oil 8 volumes, $n = 1.526$; in a medium of this refraction, the middle lamella (*M*) is clearly defined, but the other membranes (*I* and *O*) are invisible. The tube is slightly raised from sharp focus; the inner thickening (*I*) of the collenchyma walls is less refractive than the outer thickening (*O*) and appears less brightly illuminated in *A* and *B*.

properties of these media. Glycerine, on the other hand, causes a slight swelling of the walls, but this is of advantage, in this case, in bringing out the details sought.

3. PERFORATIONS IN CLOSING MEMBRANE OF PITS

The minute perforations through the closing membranes of pits, as in case of the bordered pits of conifers, can be readily demonstrated in the following manner: place a few drops of a

dilute solution of xylol dammar (mounting consistency diluted about twenty times) on the transverse face of the dry woody tissue to be tested. Section immediately to 10 μ and mount in glycerine. The perforations (FIG. 4) each with a small globule of dammar in or attached to it, are then easily visible in the glycerine medium. The cover glass may be cemented with gold size, after the manner of glycerine permanent mounts, and the preparation will keep for at least several weeks, often improving on standing a few days; but the slide should always be kept face upward.

In mounting tissues in highly refractive media, care should be taken to press the cover slip down tightly against the tissue, to exclude any excess liquid from above the section. With quinidine, for example, an effect of chromatic aberration may be produced by a film of the liquid between the lignified membranes of the section and the cover slip.

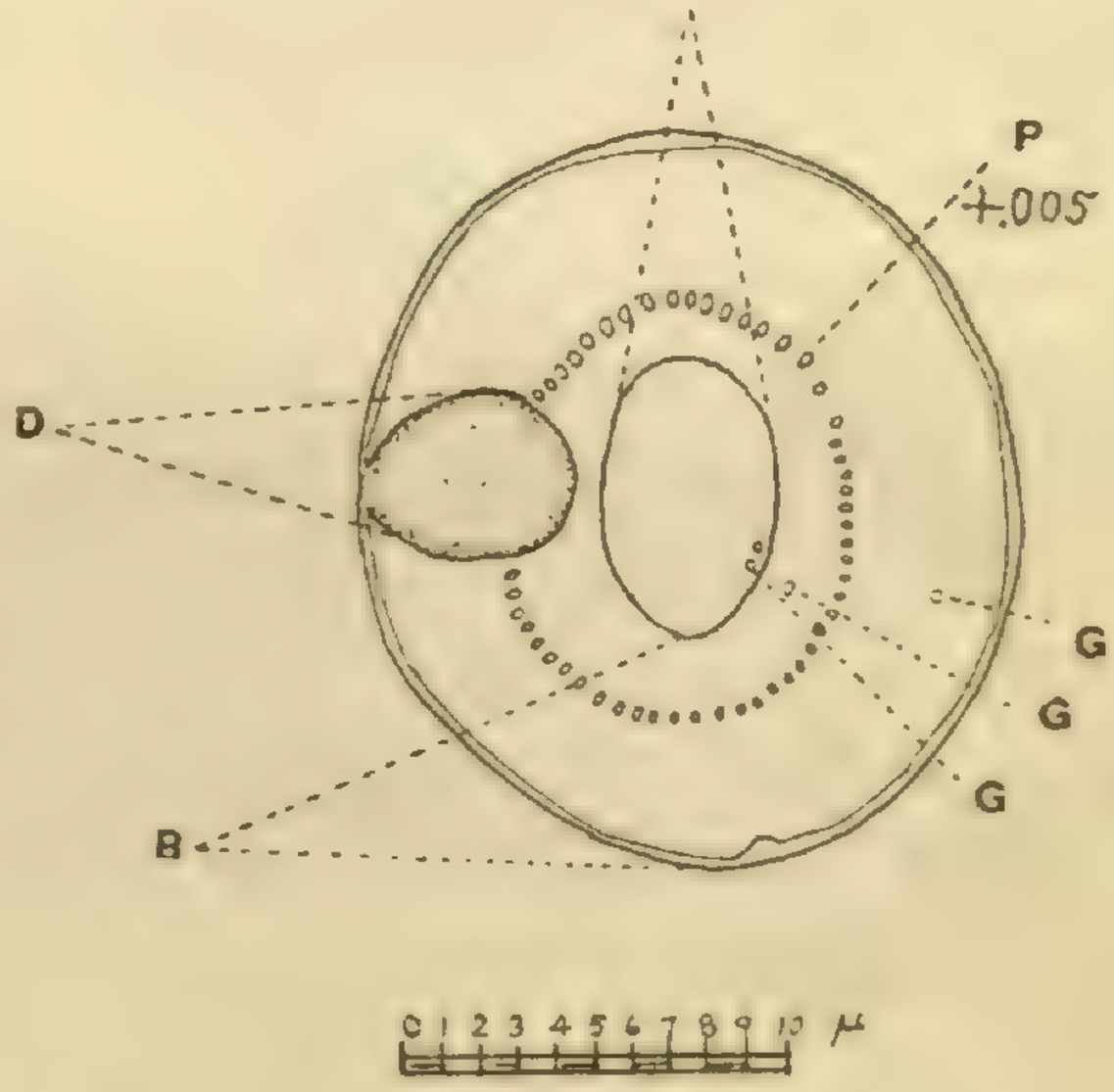

FIG. 4. Bordered pit of sugar pine, *Pinus Lambertiana*, after treatment with dammar to bring out perforations; *D*, a large globule of dammar floating partially free in the glycerine within the border (*B*); *P*, perforations through the closing membrane, arranged in a circle at the edge of the torus and visible through the transparent border; *G*, globules of dammar detached from perforation at edge of torus and floating free in the glycerine; *O*, orifice.

V. SUMMARY

1. In the fully developed tissues examined, the refractive index of the material of which any given cell-membrane or cell-content is composed is fairly constant with uniform conditions of temperature; but during the growth of a tissue the refraction of its constituent materials may change enormously. Such changes in refraction are evidently associated with corresponding changes in the chemical composition.

2. The indices of refraction of the various membranes and other elements, of which mature plant tissues are composed, differ greatly from one another, and a given tissue complex will

rarely if ever have a single refractive index. A fair average, however, would be about 1.53, or .01 above that of Canada balsam.

3. Most tissues readily absorb water and other refractive liquids, in differing amount according to the hygroscopic qualities of the tissue. This causes the refraction of the mass (tissue substance + imbibition liquid) to deviate correspondingly from that of the tissue substance. The refractive index of the membrane mass is highly sensitive to physical changes of this kind.

4. The laws of refraction have their special application to the investigation of both the anatomical characters and the physical and chemical properties of plant tissues.

5. With average sections, clearer definition is obtained when the index of refraction of the medium is below, rather than above, that of the tissue substance. A difference of at least .05 between tissue mass and the medium in which it is mounted is desirable to obtain clear definition of small perforations and similar minute details, and highly refractive media such as styrax, tolu, and quinidine bring out such details with the greatest possible clearness; in moderately thin sections, a difference of .005 is sufficient for the definition of general outlines, and may give clearer definition for general features than a greater difference in refraction.

6. In selecting a medium, to obtain a given difference in refraction between it and the tissue mass, due allowance must be made for the deviation in refraction brought about by the imbibition of liquid by the tissue.

YALE UNIVERSITY

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The physical factors in the growth of the tomato

D. T. MacDougal

The tissues of animals and of the greater number of plants accumulate carbohydrates, proteins, salts and other solids during the course of growth in such manner that the relative dry weight of an organ is least in the embryonic or earlier stages, and increases progressively so that the proportion of solid material is highest and of water is lowest at maturity.

The stems and leaves of succulents and such berry-like fruits as the tomato (*Lycopersicum*) have been found to reverse this relation,* and melons, mushrooms and similar structures probably do the same.

Tomatoes 14–18 mm. in diameter grown at the Coastal Laboratory, Carmel, California, were found to contain but 87 per cent of water, while mature fruits consisted of 91 per cent water and 9 per cent solid material. An analysis by Albahary gave 93.63 per cent of water in young tomatoes and 94.3 per cent in ripe fruits.†

In addition to the measurements already published, it seems desirable to give the data secured in 1919, to make further comparisons between the apparent growth as found by the increase in the diameter of the fruits, and to record the actual increase in volume,‡ and to formulate an explanation of growth based upon the osmotic and colloidal action of the plasmatic substances under the influence of cell-sap of varying composition.

Vigorous plants bearing fruits in all stages were available in August and September, 1919, and suitable stages were erected

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* MacDougal, D. T. Hydration and growth. Publ. Carnegie Inst. Washington, No. 297, 1920. See especially pages 166–172. Also, Hydration and growth, Proc. Amer. Phil. Soc. **58**: 346–373. 1919.

† Albahary, F. M. Etude chimique de la maturation du *Lycopersicum esculentum* (Tomate). Compt. Rend. Acad. Sci. Paris, **147**: 146–147. 1908.

‡ Note. In a discussion of this subject in the Proc. Amer. Phil. Soc. **58**: 367, 1911, the formula for obtaining the volume of a sphere, 4/3 (PiR^3) was erroneously given as (PiR^3).

so that small green fruits were resting securely on cork blocks. The vertical swinging arm of an auxograph also tipped with cork was now brought to rest on the upper surface of the fruit. Any variation in volume would be denoted by a deviation of the pen tracing from a horizontal line. A full description of this apparatus is given in connection with *f.* 1 of the publication cited above.

The temperatures in this and in my other work on growth and swelling were taken by mercurial thermometers thrust into tissues or in contact with the bodies under observation. In the present instance small thermometers of the "clinical" type were thrust into fruits similar to those being measured and remained there during their development, causing but little divergence from normal morphology. The fruit stood between 15 and 20° C. during the experiments, which was on an average 8–10° below the optimum for these plants, but the relative humidity was favorably high.

The points to be presented may be demonstrated by the action of two fruits which were kept under continuous measurement, one for thirty-eight and the other for thirty-five days.

Fruit No. 1 had a diameter of 6 mm. and a volume of 113 cu. mm. when its measurement was begun, and its volume increased at the rate of 130 cu. mm. daily for six days, 402 cu. mm. for the following seven days, 409 cu. mm. for seven days, 560 cu. mm. for nine days and 930 cu. mm. for the last 9 days, at which time the total volume was 19,864 cu. mm.

The rate of increase of the diameter of these fruits during the same periods was 0.8 mm., 1 mm., 0.55 mm. and 0.6 mm. daily. A graph plotted from these daily rates would give a highly erroneous impression as to the actual course of accession of material to the fruits, which is the essential feature of growth. If the rate of growth be multiplied by twenty-five and placed in a table above the average daily increase in volume for the same period, a comparison may be made without the aid of a graph.

It is to be seen that the rate of increase in the diameter of the

Rate of increase	First week	Second week	Third week	Fourth week	Fifth week
Diameter	20	25	14	15	16
Volume	22	57	58	63	103

fruits at the maximum was not double the lowest rate, the highest occuring while the fruit was very small. Increase in volume, on the other hand, was progressively greater and as the fruit neared maturity water and material were being brought in nearly five times as fast as in young fruits. This delayed maximum might be connected with the low temperatures under which the development took place, as the highest rate of accession of material to fruits in 1918 at higher temperatures came somewhat earlier, although subsequent to the maximum increase in diameter.

A second fruit measured for thirty-five days was 8 mm. in axial diameter at the beginning and had a volume of 268 cu. mm. It increased 0.9 mm. in diameter and 167 cu. mm. daily for a week, 0.9 mm. daily for the second week with an accretion of 492 cu. mm., 0.7 mm. daily with an accretion of 412 cu. mm. in the third week, a rate of 0.67 mm. daily with an accretion of 1045 cu. mm. in the fourth week, and 0.3 mm. daily with an accretion of 600 cu. mm. in the last week.

A comparison of increases in diameter and volume is given below:

Rate of increase	First week	Second week	Third week	Fourth week	Fifth week
Diameter	27	27	21	20	9
Volume	27	56	59	150	185

The increase in diameter was at a rate which did not vary widely until at the last, when it dropped to less than half that which had previously prevailed. The rate of increase in volume rose steadily until at the end it was seven times as great as during the first week. The accretion is visualized as forming a layer on a globe, the volume of the fruit at any time being determined by the use of the formula $V = 4/3\ (PiR^3)$. A layer of a given thickness on a large fruit would obviously include a much greater amount of material than a layer of similar thickness on a small fruit.

The mechanical features of the growth of a storage body, as a fruit must be considered, are something different from those which prevail in a stem with its successively developing members or internodes, or in leaves which proceed to a definite average size

on maturity. In both types of growth the rate depends upon, or is influenced by, the amount of growth that has previously taken place, as has been demonstrated by Reed in his measurements of growth of the stems of apricot trees.

The stems of the tomato are enlarging during the growth of the fruits, the leaf surfaces are increasing and the pedicels of the fruits show an increasing cross section, so that not only is an additional amount of water and material available but its translocation may be facilitated.

It would be erroneous however to consider the fruits as reservoirs which passively receive the solutions poured into them through the stems. The fruits are in fact largely made up of rapidly enlarging masses of thin-walled cells which control absorption of material as occurs in living tissues. Liquids are drawn into these cells, not forced.

The forces which operate to carry water and solid material into a fruit may be grouped under osmosis and imbibition.

The freely soluble sugars which constitute about 9 per cent of the dry weight of young fruits and 38 per cent of ripe fruits, according to the analyses of Albahary, would operate to set up and maintain a turgidity that would probably reach eight to twelve atmospheres, and the attractive force of these substances would be one of the main factors in drawing material into the fruits.

It is well known, however, that fruits may withdraw water from stems that are relatively drier, and that roots may take up water from soils in which the osmotic action would be greater. To account for such action we must look to imbibition, the phenomena by which colloidal matter, such as jelly or wood, absorbs water or solutions and swells as a consequence of the hydration or addition of molecules of water to the aggregates of molecules of solid matter in their intimate structure, for growth under such circumstances.

Extensive investigations at the Desert Laboratory show that the living matter of plants is a mixture of albuminous substances and of pentosans or mucilages. Furthermore, parallel experiments with mixtures made in the laboratory show that in taking up water the plant behaves like a sac containing albumin and mucilages. It is necessary for a clear understanding of the action of the

plasmatic mass to realize that the albumin and mucilage may be taken to be in an interwoven meshwork, or if in suspension in separate globules.

This being the case, one may take up water and swell, or lose water and shrink, while the reverse action takes place in the other, which might also remain inactive. Thus the albumins swell most in acids or under the influence of free hydrogen ions, although being amphoteric they may also swell in hydroxyl ions or under the action of bases, while they are not very active in solutions of amino-compounds. The mucilages on the other hand are weak acids, swelling but little in acids, more under the action of hydroxyl ions or bases, still more in water, and reaching a maximum in amino-compounds.

Mixtures of mucilages and of albumins will, in the main, show reactions determined by the element which makes up the largest proportion of its mass. It follows therefore that the growing cell-masses of plants show swelling, hydration and growth reactions determined by the mucilages or pentosans, as modified by the albumins, acids, and salts present.

When we take up the facts disclosed by chemical analyses of tomatoes, we discover five things which must be taken into account in any attempt to make a physical-chemical explanation of growth These are as follows: (1) the proportion of sugar, including the mucilages, in the dry material increases from 9 to 37 per cent in the stage of enlargement including the formation of the seeds; (2) the acids, which include malic, phosphoric and citric, increase toward maturity; (3) the albumins decrease with development; (4) the ash or metallic bases increase from 4.5 to 10.75 per cent of the dry weight; and (5) the proportion of cellulose lessens as the fruit proceeds toward maturity.

If due weight be given to these factors or agencies the procedure in growth may be determined. Thus in the earlier stages the total albumins constitute less than 3 per cent of the dry weight and the sugars over 10 per cent, of which at least one third may be taken to be pentosans or mucilages. The colloidal mixture of equal parts of the two—mucilages and albumins—might be capable of showing a hydration capacity of over 3,000 per cent in a cell sap containing any one of a number of amino-acids which are

invariably present in cell-masses of this kind. The hydrogen ion concentration and the proportion of salts or bases is still low and their effect on the swelling would be limited. It would therefore be possible for these young fruits to make a notable amount of growth or expansion upon imbibition by the protein-pentosan plasma in a juice relatively low in salts and in acids.

Development and increase in size would however be attended by a lessened albumin content, making the plasma react more like agar in which hydration is lessened by salts and by acids, and imbibitional swelling would be notably decreased.

The accumulation of sugars in the cells occurring concurrently with lessened imbibition serves to set up an osmotic mechanism by which an increasing turgidity would result, serving as a distentive agency in the later stages of growth more than replacing the waning capacity for imbibition, and the action of osmosis in these fruits might have a heightened effect by reason of the fact that the cell walls of much of the fruit become "pectinated" and the proportion of cellulose becomes less, according to the analytical results of Albahary. This last named feature is the reverse of that in stems or vegetative tissues in which the cell walls become heavier and more indurated with progressive development.

The above conditions in the fruits are fully sustained by the following set of swelling reactions, which are entirely characteristic of a pentosan-protein colloid high in mucilages of the first group.

SWELLING OF RADIAL SLICES OF GROWING FRUITS 25–35 MM. IN DIAMETER

	Propionic acid	Alanine	Phenyl-alanine	Glycocoll	Water
0.01M	10%	25%	25%	25%	21%

In a later stage of the fruits when the skin is turning yellow, the salt content amounts to 10 per cent of the dry weight and the acidity is such that the sap has hydrogen ion concentration of a PH value = 4, while the albumins have decreased.* The results of a set of swellings are as follows:

	Propionic acid	Alanine	Phenyl-alanine	Glycocoll	Water
0.01M	16	15.5	11	15	15

* Cohn, E. J., J. Gross & O. Johnson. The isoelectric points of the proteins in certain vegetable juices. Jour. Gen. Physiol. 2: 145–160. 1919.

Regardless of other causes the acidity, high salt content and low albumin content would be sufficient to restrict absorption of water by the plasmatic colloids to two thirds the capacity shown by young fruits.

If we now turn to cultural experiments, ample confirmation is found for the conclusion that the amino-compounds which increase hydration or water absorption also facilitate or accelerate growth as measured in terms of dry weight, as found by Dachnowski and Gormley, Borowicov, Long, and Schreiner, Skinner and Beattie.*

Still one more feature of growth remains to be considered, that of certain retarding factors. The material which goes to increase the fruit of the tomato is about 90 per cent water. As water is being constantly transpired from the thin skins of these fruits, it is obvious that a hightened transpiration might throw off water at a rate which would use much of the liquid brought in by absorption and thus decrease growth. This occurs almost every day of sunshine and may result in the fruit having a lesser diameter at noon than at sunrise. Such cessation of growth in length and thickness of stems has been observed many times, and was earlier supposed to be due to the retarding action of light. It is however simply a loss of water greater than the absorption during the same time with a consequent shrinkage.

The principal conclusions supported by the foregoing may be briefly stated as follows:

1. The fruits of the tomato (*Lycopersicum*) furnish examples of development and growth without increase of dry weight.

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* See MacDougal, D. T. Hydration and growth. Carnegie Inst. Washington Publ. No. 297, 1920. See pp. 51 and 52, 63 and 64, and the following titles not considered in the preparation of that publication:

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2. The rate of increase in diameter of such globose, berry-like fruits is not a correct or even approximate measure of actual growth considered as an accretion of water and solid material.

3. The time at which the greatest increase in diameter takes place may coincide with the greatest growth as exemplified in previously described observations, but the increase in thickness is not a direct index of growth in such bodies. Actual growth varies as the cube of the radius.

4. The culmination of the rate may not be reached until the fruit is in a stage approaching maturity. The maximum accretion generally takes place in a stage subsequent to the highest rate of increase of the diameter.

5. The internal factors which determine the rate and amount of growth of the tomato include the soluble sugars and the salts or bases which increase toward maturity, and the albumins and celluloses which decrease with development, while the amino-acids, not determined, probably do not vary so widely as to affect their value as growth accelerators.

6. The conjunction of low acidity and low salt content and sugar content would give a set of conditions for high imbibitional swelling of a pentosan-protein plasma in the earlier stages of growth which would be capable of carrying the fruit to an enlargement of 3,000 to 4,000 per cent of the dry matter, as determined by previous experiments in the hydration of such colloids. Otherwise expressed, imbibition would be capable of making a colloidal body like a fruit which would consist of 97.5 per cent water and 2.5 per cent solid matter.

7. The higher salt content and acidity of older fruits would operate to lessen imbibition in the fruits, which in this stage would be high in carbohydrates.

8. The above facts support the conclusion that the distentive force in growth of young fruits is chiefly imbibition. Osmotic action may play the more important part in later stages.

9. The growth of a fruit therefore is a resultant of two groups of activities, one ordinarily classed as imbibitional and the other associated with osmosis and turgidity.

10. Young fruits include 1 to 4 per cent more solid material than mature ones, these bodies being representative of a type of

plant structure in which the dry weight does not increase with age.

11. The amino-acids induce a greater swelling or absorption of water by the cell masses of growing tomato fruits than takes place in weak acid solutions or in water. This fact is in agreement with, and is probably fundamental to, the accelerating effect of these substances on growth.

12. Continuous measurements of tomato fruits reveal slackened growth or shrinkage in the midday period corresponding to the time of greatest transpiration, and it is concluded that water absorption during this period is balanced by the loss from the surface, in accordance with the behavior of many other structures, such as trunks and twigs of trees, stems of sunflowers, joints of *Opuntia*, and leaves of *Mesembryanthemum*.

Desert Laboratory

INDEX TO AMERICAN BOTANICAL LITERATURE

1914–1919

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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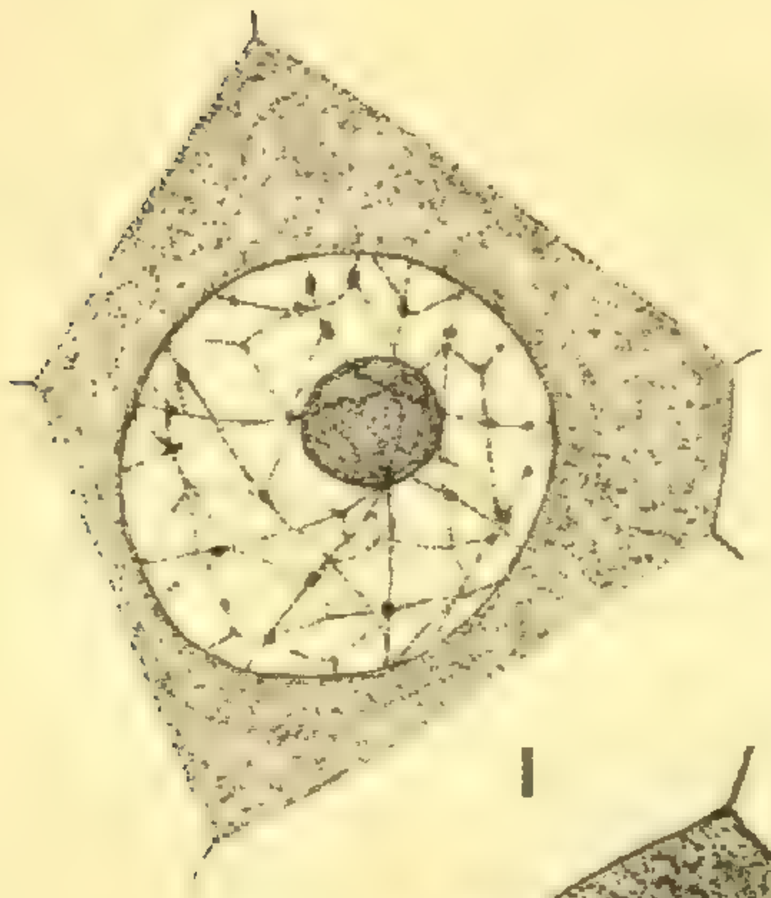

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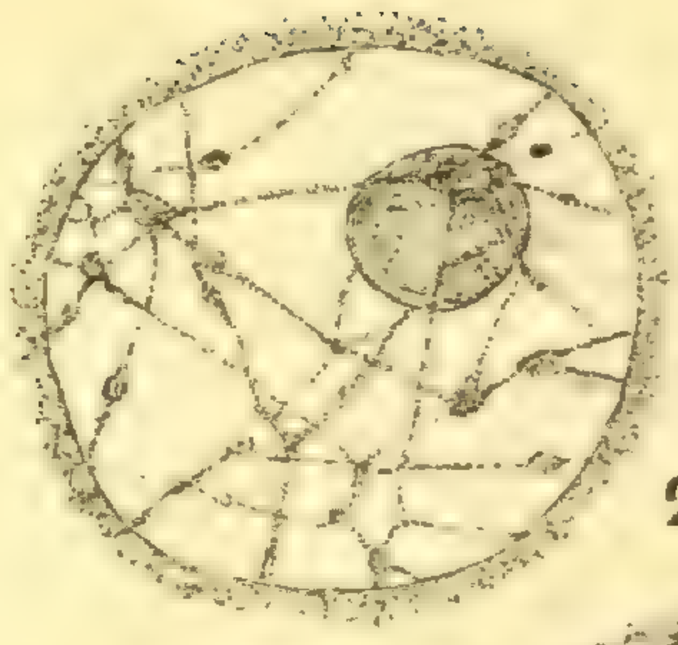

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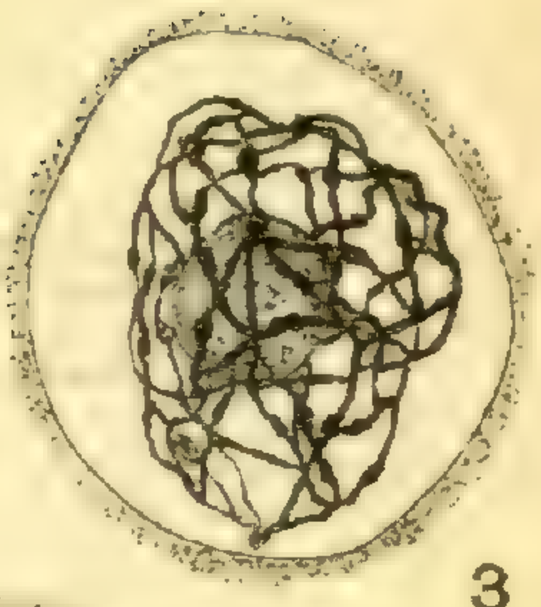

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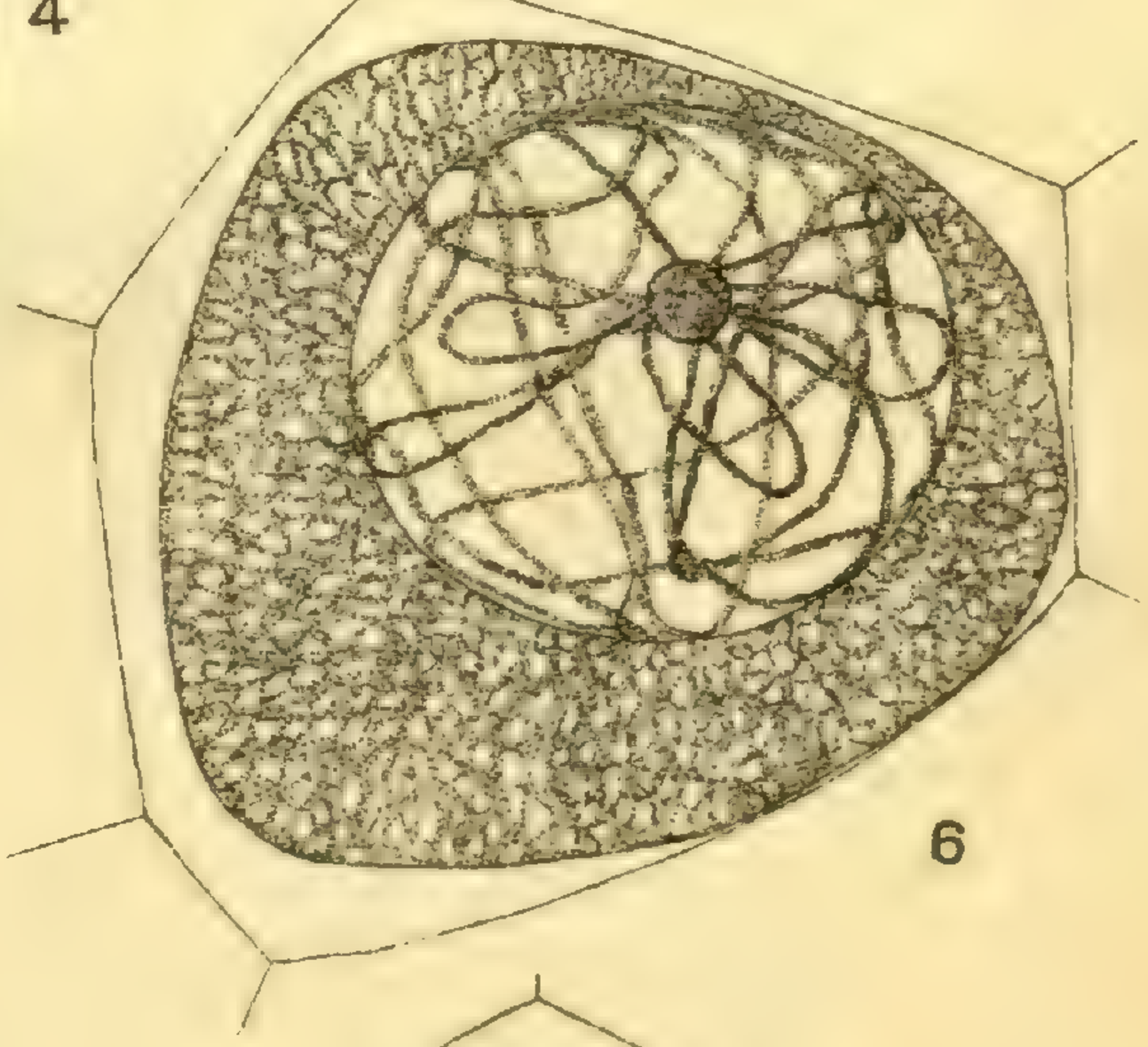

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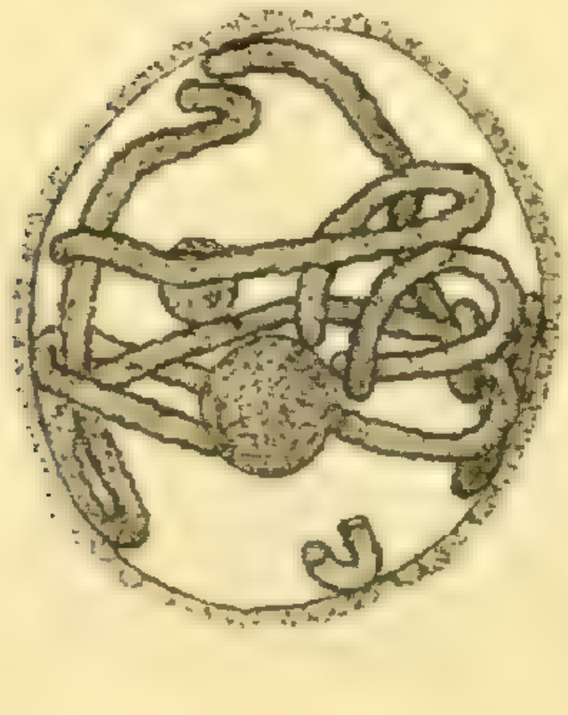

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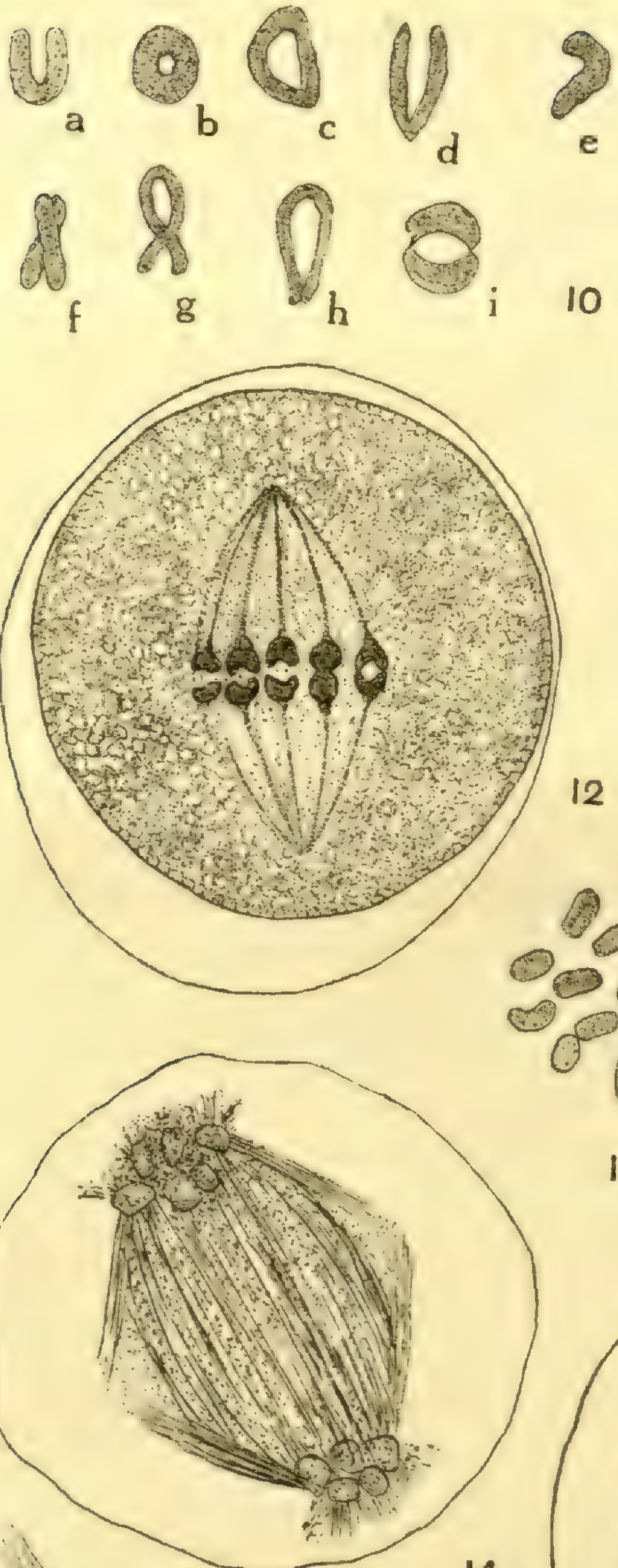
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Vol. 47 No. 7

BULLETIN

OF THE

TORREY BOTANICAL CLUB

JULY, 1920

Illustrations of six species of Riccia, with the original descriptions

CAROLINE C. HAYNES

(WITH PLATES 10–13)

A systematic account of the North American Ricciaceae will soon be published by Dr. Marshall A. Howe in the North American Flora. Among the species of *Riccia* attributed in this work to the United States the following six have not yet been adequately figured, at least from American material: *R. Donnellii*, *R. dictyospora*, *R. Beyrichiana*, *R. arvensis*, *R. hirta* and *R. Curtisii*.* It therefore seems fitting to publish in advance illustrations of these species. The data in regard to distribution and synonymy have been taken, with Dr. Howe's permission, from his manuscript; and for the sake of completeness the original descriptions, which in some cases are difficult of access, are reproduced in full.

1. RICCIA DONNELLII Aust. Bull. Torrey Club 6: 157. 1877

"Dioica maxima; fronds solida esquamosa subglauca superne maxime reticulata subtus concolore, laciniis subsimplicibus pro more discretis planiusculis siccitate canaliculatis costatis margine spinulis (serie singula) breviusculis hyalinis valde incrassatis obtusus patentibus armatis, nervo solidissimo valde incrassato subtus in media fronde terminante apice valde incrassato obtuso subdescendente, sporangiis serie singula in media fronde versus basin sitis, sporis maximis subrotundis nigris valde opacis subtuberculatis; involucris masculinis magnis valde prominentibus

* As indicated later *R. Curtisii* has recently been figured by McAllister, but chiefly as to the morphology of the sporophyte; and *R. Beyrichiana* has doubtless been illustrated by European authors under the name *R. Lescuriana* and possibly under other names.

[The BULLETIN for June (47: 231–278, *pl. 8, 9*) was issued June 23, 1920.]

subbasilaribus.—In a garden at Jacksonville, Florida, Feb., 1877.—*J. Donnell Smith*."

HABITAT: in gardens and waste places, usually on sand.

DISTRIBUTION: Florida and Texas.

EXSICCATAE: Underw. & Cook, Hep. Amer. *42*.

2. RICCIA DICTYOSPORA M. A. Howe, Bull. Torrey Club 28: 163. 1901

"Thallus simple or once dichotomous, forming irregularly gregarious patches, finally oblong or elongate-obovate, rarely sublinear, 4–10 mm. × 1–2 mm., reticulate above, light green (when dry) with at length a narrow dark-purple border; median sulcus acute and somewhat pronounced toward the apex; ventral scales entire, purple at maturity, slightly exceeding the thin submembranous ascending thallus-margins; width of transverse sections of the thallus 1.5–3 times their height, the ventral outline rounded-convex or somewhat flattened, air-canals narrow and vertical, special cells densely filled with a yellowish granular substance ('oil-body' cells) usually abundant; primary epidermal cells oval-papilliform, soon collapsing, leaving more or less persistent cup-like vestiges: monoicous; antheridial ostioles not elevated: spores brown, rather translucent, soon exposed by the rupture of the overlying parts, 95–116 μ in maximum diameter, scarcely angled, somewhat flattened, wholly destitute of wing-margins, almost uniformly areolate over entire surface, in optical section appearing densely beset on all sides with short truncate spines or papillae; areolae of the outer face 8–12 μ in width, often less perfect in the middle of the face; areolae of the inner faces so similar to those of the outer as not to be readily distinguished at first sight, yet slightly larger and less regular, with somewhat less elevated boundaries.

"On moist granite rock near Oconee River, Athens, Georgia (alt. 183 m.), Roland M. Harper, June 26, 1900, no. 68a."

HABITAT: moist granite rocks.

DISTRIBUTION: Connecticut and Georgia.

EXSICCATAE: Harper, Georgia Plants *68a*.

3. RICCIA BEYRICHIANA Hampe; Lehm. & Lindenb. in Lehm. Pugill. 7: 1. 1838

"R. *fronde carnosa oblongo-lineari bifida, supra canaliculata, margine adscendente integerrima, subtus nigro-purpurascente, apicem versus incrassata.*

"In America boreali inter Jefferson et Gainsville legit C. Beyrich. Specimina communicavit cl. Hampe.

"Frondes caespitosae, radiculis multis longis hyalinis terrae adhaerentes, 2–4 lineares, e basi angusta lineari sensim dilatatae, rarius simplices, plerumque ad tertiam partem et ultra bifidae; lobi paullo divergentes, obtusiusculi, nonnunquam iterum emarginato-bifidi. Tota frons est carnosa, apicem versus subtus magis tumida, supra canali medio angusto instructa, viridis, margine subadscendente, sphacelata, subtus membrana nigro-purpurascente vestita, integerrima. Sub epidermide hyalina tenera e cellulis hexaedris conflata adest stratum viride satis spissum. Contextus cellulosus internus est laxior, cellulis irregularibus.

Obs. Proxime accedit ad *R. hortorum* [an African species], quae distinguitur statura multo majore, fronde latiore margine undulato-crenata subtus minus tumida. *Riccia tumida* [a synonym of *R. Michelii* Raddi, a European species] differt a nostra fronde minus divisa ciliata basi planiuscula."

TYPE LOCALITY: between Jefferson and Gainesville, Georgia.

DISTRIBUTION: Massachusetts to Florida, Texas, California, and Alberta; also in Europe.

EXSICCATAE: Aust. Hep. Bor.-Am. *143* (as *R. Lescuriana*).

The original description of *Riccia Lescuriana* Aust.,* which is now considered a synonym of *R. Beyrichiana*, is as follows:

"RICCIA LESCURIANA, Aust. MSS., 1863.

"R. fronde solida subciliata orbiculata stellatim vel subcruciatim divisa incrassata, supra punctato-reticulata glauco vel cineraceo-viridi epidermide macula purpurea supra fructum notata, subtus nuda concolore vel demum purpurascente; laciniis bilobis vel di-trichotomis obcordatis lineari-cuneatisve (2–5 lin. longis, 1–2 lin. latis) leniter concavo-canaliculatis, apice emarginatis brevi sulcatis, margine hirsuto-ciliatis incrassatis obtusis subadscendentibus ad apicem subinvolutis; ciliis creberrimis brevibus albidis obtusis in statu juniori subobsoletis; fructibus sparsis non seriatis subbasilaribus, sporis fusco-atris angularibus reticulatis: gemmis? numerosis ellipticis aterrimis in frondis facie superiori versus loborum apicem positis quam sporis triplo minoribus.—*Hep. Bor. Amer. Exsic. ined.*, *N.* 143.

* Proc. Acad. Nat. Sci. Philad. **1869**: 232. 1869.

"Var. α, cruciata. Fronde cruciatim parce divisa, laciniis ciliisque brevissimis.

"Var. β, trichotoma. Fronde magis divisa, laciniis ciliisque longioribus.

"The var. α occurs almost exclusively on damp ground in cultivated fields; the var. β on rocky soil, associated with the var. of the preceding species [*R. arvensis*, var. *hirta*, now *R. hirta*], and with *R. sorocarpa* and *R. lamellosa* [now considered distinct from the European *R. lamellosa* Raddi and known as *R. Austini* Steph.].

"*R. palmata*, Lindbg., a closely related species [now included among the synonyms of *R. Michelii* Raddi], is described as having the frond palmately lobed and the divisions broadly sulcate, with the ciliae arranged in a single series. *R. Bischoffii*, Hu[e]ben. [a European species], has the margin of the frond membranaceous, the lobes much expanded, and spores twice as large. The var. α has much the appearance of *R. bifurca*, Hoffm. [a European species], as figured in Lindbg. Monogr. d. Ricc. T. XX, f. 1, but that has the margin of the frond naked."

4. RICCIA ARVENSIS Aust. Proc. Acad. Nat. Sci. Philad. 1869: 232. 1869

"R. fronde solida subciliata incrassata orbiculari subradiatim pluries divisa subgregario-imbricata in diametro 4–8 lineari, supra papuloso-reticulata obscure viridi vel demum secus margines purpurea, subtus nuda vel obsolete squamosa valde obtuseque carinato-incrassata ob sporangia tumentia valde nodosa; lobis obtusiusculis obsolete emarginatis lineari-ellipticis vel fere linearibus dichotomis versus apicem incrassatum leniter dilatatis, apice in statu juniori subadscendentibus vix canaliculatis, in aetate horizontalibus subcompresso-acuminatis evidentius lateque sulcatis, margine planis acutis (in adspectu incrassatis obtusisque); ciliis albidis brevissimis omnino inconspicuis subobsoletisve; fructibus primum versus apicem loborum infra canalem agregatis, sporis angularibus fusco-atris reticulato-muricatis.—*Hep. Bor. Amer. Exsic. ined., No.* 141.

. . . . . .

"On damp ground in cultivated fields . . . about Closter, New Jersey, common.

"The canal occupies about ⅓ of the upper surface of the frond, and has a plane or slightly convex bottom with abrupt sides.

That portion of the frond between the canal and the acute margin is slightly convex above *as if thickened*. The typical form appears to be near *R. paradoxa*, De Not. [now included among the synonyms of *R. Michelii* Raddi], but that is described as being a smaller species, and the spores are said to be light-red. . . . The sporangia are placed rather towards the apex of the lobes as in *R. palmata* Lindbg.; which appears to be a larger species, with the lobes of the frond concave-canaliculate above, &c., and seems to be intermediate between this and the following species [*R. Lescuriana* Aust., now *R. Beyrichiana*]."

HABITAT: in fields and wet broken ground; common.

DISTRIBUTION: New Hampshire and Ontario to Indiana and Texas.

EXSICCATAE: Aust. Hep. Bor.-Am. *141;* Haynes, Am. Hep. *2, 98.*

5. RICCIA HIRTA Aust.; Underw. Bot. Gaz. **19**: 274. 1894

Riccia arvensis hirta Aust. Proc. Acad. Nat. Sci. Philad. **1869**: 232. 1869.

"Var. β, hirta. Statura majora, fronde subtus magis purpurea et squamigerula margine evidentius ciliata, supra omnino hirta.—*Hep. Bor. Amer. Exsic. ined., No.* 142.—*R. hirta*, Aust. MSS. 1864:

". . . (the var.) in rocky places about Closter, New Jersey.

". . . The var. differs from *R. cilifera*, Link. [a synonym or variety of *R. Bischoffii*], in the fronds being purple and more or less scale-bearing underneath, and not membranaceous on the margin."

HABITAT: moist rocky ground.

DISTRIBUTION: Connecticut to Louisiana and Texas.

EXSICCATAE: Aust. Hep. Bor.-Am. *142* (*p.p.*, as *R. arvensis* var. *hirta*).

6. RICCIA CURTISII James (Aust. Proc. Acad. Nat. Sci. Philad. **1869**: 231. 1869, as synon.) Steph. Bull. Herb. Boiss. **6**: 369. 1898

This was originally described as representing a new genus, *Cryptocarpus* (afterwards changed to *Thallocarpus* by Lindberg*), as follows:

"CRYPTOCARPUS, (gen. nov.) Aust. MSS., 1864.

"Frons laxe spongioso-reticulata, irregulariter subpalmatim lobata, tenuis, epidermide haud distincta. Costa nulla. Radices

* Not. F. et Fl. Fenn. **13**: 377. 1874.

intus non papillosi (ut in *Sphaerocarpo*), longissimi, intertexti. Fructus in frondis substantia immersus (ut in *Riccia*). Sporangia depresso-globosa, singulatim nata, non libera. Calyptra stylo nigro persistente coronata. Sporae 4-jugae (ut in *Sphaerocarpo*), vix solutae, in aspectu singulae et profunde quadrilobae.

"A genus intermediate between *Riccia* and *Sphaerocarpus*, having the characters of vegetation and spores of the latter, while the fruit is immersed in the frond as in the former genus. Represented by a single species, which occurs both in the Southern States and in France.

"CRYPTOCARPUS CURTISII, Aust. MSS., 1864.

"*Riccia Curtissi*, James, in Herb. (fide Curtis).

"Fronde caespitosa valde imbricata fibroso-papulata, laciniis inciso-lobulatis margine crenatis; sporangiis maximis in statu siccati latentibus sed frondes humefactae sunt in substantia earum ut maculis nigris apparentibus; sporis fusco-nigris valde muricatis.

"On moist ground, South Carolina, Ravenel (in Herb. Sulliv., 1849) North Carolina, Curtis (l.c., 1853). 'Montand après Marseille' (Herb. Lanning, 'ex. Herb. Torrey').

"To the naked eye the dried specimens look like little heaps of some filamentose conferva. In this state the frond is very brittle, and, on account of its loose texture, appears to be deeply pitted and fibrose and papulose above. Upon moistening the specimens the fronds become tough (much as in the *Anthoceroteae*), the upper surface looses its pitted appearance, and the interstices (apparent fibres) between the large cells close up; and the fruit, which was completely hidden before, now appears as a black spot in the substance of the frond. Upon re-drying the specimens the fronds become much thinner than they were at first, and the fruit remains visible, protruding from the upper surface. The frond is larger than in *Sphaerocarpus Michelii*, from the Southern States, but lobed and reticulated in the same manner. The extreme apices of the lobes are often suddenly contracted and subsolid (much as is often seen in the Anthoceroteae). The base of the divisions are contracted and subsolid, and the rootlets are smooth on the interior surface as in *Sphaerocarpus*. The divisions are flabelliform, and palmately or incised-lobed, and lie

so closely over one another as to be separated with difficulty, the upper ones, by their numerous long rootlets, knitting firmly to the pitted surface of those immediately beneath them. The lobes are crenate and obtuse, not emarginate, extremely thin and hyaline. Spores firmly united in fours into a sort of *coccus* which is deeply 4-lobed, and very beautiful under the lens,—more deeply lobed than in *Sphaerocarpus terrestris* and more finely reticulated and papillose."

TYPE LOCALITY: North Carolina.

DISTRIBUTION: North Carolina to Florida and Texas.

ILLUSTRATIONS: Bull. Torrey Club 43: *pl. 4.* 1916.*

EXSICCATAE: Underw. & Cook, Hep. Am. *43* (as *Thallocarpus Curtisii*).

Appreciative thanks are due to Dr. Howe and Professor Evans for valued assistance, to the Rev. E. E. Brooks for a translation, and to Mr. Severin Rapp for specimens of *R. Donnellii* and *R. Curtisii*, collected at different periods of the year.

HIGHLANDS,
NEW JERSEY

Explanation of plates 10–13

PLATE 10

RICCIA DONNELLII Aust.

FIG. 1. Dorsal side of an unusually large mature plant, showing several capsules; in older parts, walls rupturing and spores scattering; hyaline marginal pappillae plainly visible. Drawn from dry material. × 4.

FIG. 2. Ventral side of a thallus, showing beginnings of tuberiferous or resting stage not uncommonly met with in collections made in January and February. Drawn from fresh material. × 4. Austin's original description mentions this tendency to thicken ventrally at the apex of the axis, which is "greatly thickened and blunted as it grows downwards." This fact has been lost sight of in more recent descriptions.

FIG. 3. Portion of epidermis, with marginal cilia. × 47.

FIG. 4. Dorsal side of old fruiting plant, through the transparent wing of which the well-developed stalked tuber is seen arising from the ventral apex of the costa. × 4.

FIG. 5. Unusually well-developed tuberous prolongation of the costa, showing rudimentary scales. ×19.

FIG. 6. Cross-section near apex of a tuber. × 9.

FIG. 7. Outline of a cross-section of thallus. × 19.

FIG. 8. Portion of epidermal layer, in cross-section, drawn from fresh material. × 120.

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* See McAllister, F. The morphology of *Thallocarpus Curtisii*. Bull. Torrey Club 43: 117–126. *pl. 4.* 1916.

FIG. 9. Scale. × 33.

FIGS. 10 and 11. Spore, outer and inner faces, showing irregular and anastomosing ridges. × 265.

FIG. 12. Spore, showing outer face with light reticulations or shallow pits in middle portion. × 265.

FIG. 13. Spore, showing outer face with markings similar to those of 10. × 265.

FIG. 14. Spore, showing inner triangular faces. ×265.

FIG. 1 was drawn from a specimen in the herbarium of the New York Botanical Garden, from Jacksonville, Florida, Underwood & Cook, Hep. *42*; FIGS. 2 and 3, from a specimen collected by Severin Rapp, at Sanford, Florida, February 7, 1913; FIGS. 6, 8, and 9, from a specimen collected by Severin Rapp, at Sanford, Florida, May 9, 1912; FIGS. 4, 5, 7, 10, and 11, from a specimen collected by Severin Rapp, at Sanford, Florida, January, 1904, and communicated by Herr F. Stephani; FIGS. 12, 13, and 14, from a specimen in the herbarium of the New York Botanical Garden, collected at Jacksonville, Florida.

PLATE 11

FIGS. 1–5. RICCIA DICTYOSPORA M. A. Howe

FIG. 1. Plant colony, drawn from fresh material. × 4.

FIG. 2. Plant twisted in growth, showing latero-ventral scales. × 33.

FIG. 3. Outline of cross-section of thallus. × 19.

FIG. 4. Spore, outer face. × 390.

FIG. 5. Optical section of spore, showing difference in height of papillae, the the upper side of figure representing the outer face. × 390.

FIGS. 1 and 3 were drawn from plants collected by C. C. Haynes, on West Rock, New Haven, Connecticut, October 12, 1911; FIGS. 2, 4, and 5, from type material, R. M. Harper *68a*, Athens, Georgia, June 26, 1900.

FIGS. 6–11. RICCIA BEYRICHIANA Hampe

FIG. 6. Plant colony, drawn from fresh material. × 4.

FIG. 7. Outline of cross-section of thallus, showing cilia. × 19.

FIG. 8. Cells and cilia seen in cross-section of thallus. × 19.

FIGS. 9 and 10. Spore, outer and inner faces. ×390.

FIG. 11. Spore in profile showing bold markings on outer face. × 390.

FIGS. 6, 7, and 8 were drawn from a specimen collected by C. C. Haynes, on West Rock, New Haven, Connecticut, October 21, 1911; FIGS. 9, 10, and 11, from a specimen collected by Annie Lorenz, at Hartford, Connecticut.

PLATE 12

FIGS. 1–6. RICCIA ARVENSIS Aust.

FIG. 1. Plant colonies, drawn from fresh material. × 4.

FIG. 2. Outline of cross-section of thallus. × 20.

FIG. 3. Portion of epidermal layer in cross-section. × 155.

FIG. 4. Portion of epidermis, showing rarely occurring cilia. × 87.

FIG. 5. Spore, outer face, showing areolate-alveolate markings and crenate or crenulate wing. × 390.

FIG. 6. Portion of wing with crenulate margin seen in optical section. × 390.

FIG. 1 was drawn from a specimen collected by C. C. Haynes, at Hartford, Connecticut, October 20, 1911; FIG. 2, from a specimen collected by Fred Donaghy,

Harrodsburg, Indiana, February 20, 1915, in the herbarium of the New York Botanical Garden; FIGS. 3 and 4, from a specimen collected by C. C. Haynes, Highlands, New Jersey, October 7, 1911; FIG. 5, from a specimen collected by A. W. Evans, Orange, Connecticut, October, 1899, Haynes, Am. Hep. 2; FIG. 6, from a specimen collected at Closter, New Jersey, by C. F. Austin, Hep. Bor.-Am. 141.

FIGS. 7–13. RICCIA HIRTA Aust.

FIG. 7. Plant colony, drawn from fresh material. × 4.

FIG. 8. Outline of cross-section of thallus, showing two cilia. × 33.

FIG. 9. Portion of epidermal layer in cross-section. × 265.

FIG. 10. Portion of epidermis showing two cilia. × 87.

FIG. 11. Spore, outer face. × 390.

FIG. 12. Spore, inner faces. × 390.

FIG. 13. Outline of spore in profile showing papillae on outer face, represented by upper side of figure. × 390.

FIG. 7 was drawn from a specimen collected by Annie Lorenz, Meriden, Connecticut, November 12, 1911; FIGS. 8, 9, 10, and 11, from a specimen collected by Annie Lorenz 956, West Hartford, Connecticut, October 8, 1911; FIGS. 12, and 13 from a specimen collected by F. V. Coville, Georgetown, District of Columbia, December 24, 1889.

PLATE 13

RICCIA CURTISII James

FIGS. 1 and 2. Plant colonies, showing archegonial (larger) and antheridial (smaller) plants. × 4.

FIGS. 3 and 4. Outlines of simple plants, showing capsules. × 4.

FIGS. 5 and 6. Epidermal cells, dotted and heavy lines indicating lamellae, forming walls of the air-chambers. × 240.

FIG. 7. Outline of portion of thallus in cross section. × 4.

FIG. 8. A portion of thallus in cross section. × 33.

FIG. 9. Spore tetrad, showing very blunt papillae and very low connecting basilar ridges. × 307.

FIG. 10. Spore, covered with more conical papillae. × 307.

FIGS. 1, 3, 5, and 9 were drawn from a specimen collected by Mary Young, Austin, Texas, March 3, 1914; FIGS. 2, 6, and 8, from a specimen collected by Severin Rapp, Sanford, Florida, May 2, 1912; FIGS. 4 and 10, from a specimen collected by Severin Rapp, Sanford, Florida, April 12, 1911; FIG. 7, from a specimen collected by Severin Rapp, Sanford, Florida, December 12, 1911.

A week in eastern Texas

ROLAND M. HARPER

(WITH FIVE TEXT FIGURES)

INTRODUCTION

Diversity of the coastal plain in Texas.—Of the fifty or more geographical divisions of the coastal plain of the eastern United States, differing significantly in soil, topography, vegetation, etc., very few extend through more than two states, or are as much as two hundred miles in longest dimension; and none of the divisions in Texas, with the possible exception of the red hills in the extreme east, can be closely correlated geographically with anything east of the Mississippi River. The number of natural regions in the Texas coastal plain, between the Red River on the north, the Sabine on the east, and the Rio Grande on the southwest, cannot yet be stated with exactness, but must be at least a dozen. The first noteworthy attempt to map them seems to have been that of Dr. R. H. Loughridge, in his report on cotton production in Texas, in the 5th volume of the Tenth Census, 1884 (colored map facing page 671).* This covered the whole state, and is probably more accurate for the coastal plain than for the remainder, for there were no railroads in the western half of the state in those days. In the accompanying text the various regions were described, with reference to soils, vegetation, agriculture, etc.

In 1900 Robert T. Hill published in "Topographic Folio No. 3" of the U. S. Geological Survey an excellent regional map of Texas and part of New Mexico and what is now Oklahoma, which has been copied by some of the other writers referred to below;† but

* A worthy successor to Loughridge's map is a colored soil map of the principal cotton-producing regions of the United States, by H. H. Bennett, on page 8 of the section of the folio Atlas of American Agriculture devoted to cotton, published by the U. S. Department of Agriculture early in 1919.

† The same map appeared the following year as Plate 1 (opposite page 26) of a ponderous monograph on the Black and Grand Prairies of Texas by the same author, which constitutes Part 7 of the 21st Annual Report of the U. S. Geological Survey, and is more accessible than the Topographic Folio.

he recognized at that time only four or five divisions in the coastal plain. Vernon Bailey, in his "Biological survey of Texas" (U. S. Dept. Agriculture, N. Am. Fauna No. 25. Oct., 1905), discussed the distribution of plants and animals (mainly the latter) in the same territory mapped by Hill, with special reference to climate, paying very little attention to the pronounced contrasts of soil, and using a colored map that treats the whole coastal plain of Texas, east and north of a line drawn through Austin and Victoria, as a unit, under the designation of "Austroriparian" area. (The "life-zone" system of the U. S. Biological Survey, being based on climatic factors, does not work out very satisfactorily in non-mountainous regions.) In the text, however, Bailey admits that the country near the coast has some subtropical characteristics, and that the flora of the black prairie, coast prairie, marshes, islands and beaches is different from that of the wooded portions of the humid area.

Another important geographical work, covering approximately the same territory as the present paper, is "Geology and underground waters of the southeastern part of the Texas coastal plain," by Alexander Deussen (U. S. Geol. Surv. Water Supply Paper 335, with 365 pages and 9 plates. 1914). This includes a pretty good though brief account of the regional geography, with a few notes on the forest growth. Additional information of a similar nature may be gathered from several state and government geological reports which do not need to be enumerated here, and from the government soil surveys of various counties.*

A recent study in regional geography, covering the whole state, is "Studies in the industrial resources of Texas," by L. H. Haney and others, constituting University of Texas Bulletin 3 of the 1915 series, with 105 pages, and including a map which divides

*Since this manuscript was sent to the editor there has appeared University of Texas Bulletin 1869 (i.e., no. 69 of the 1918 series), on The geology of East Texas, by E. T. Dumble, comprising 396 pages, 9 half-tone plates, and 3 loose maps. (It is dated Dec. 10, 1918, but does not seem to have been published until March, 1920.) On page 271 is mentioned a more or less interrupted tongue of the coast prairie extending inland to the northwestern portion of Liberty County, but the information came too late to be utilized in drawing my map, and is hardly definite enough anyway. Sundry other references to prairies, mounds, salt licks, rock outcrops, etc., scattered through the bulletin are of some botanical interest.

the state into eleven regions and indicates land values for each county by shading.*

Geological and climatic relations.—From Pennsylvania to Alabama there is a vast geological hiatus at the fall-line, between the metamorphic rocks of the Piedmont region (and Triassic sedimentary strata for part of the distance across North Carolina) and the unindurated Cretaceous and later strata of the coastal plain. From Alabama to Illinois and Oklahoma the coastal plain formations at the fall-line abut against Paleozoic strata, which although mainly horizontal and unaltered are characterized by an abundance of hard rock, something that is relatively scarce in the coastal plain. In Texas, however, the fall-line is hard to define, for strata of Cretaceous age in practically uninterrupted series extend from the unquestioned coastal plain area far into the interior, merging into the southern extremity of the Great Plains, a province whose rocks are mostly of the same age as the coastal plain strata, but nearly as hard on the average as those of Paleozoic age. But in Texas it is customary to place the boundary of the coastal plain somewhat arbitrarily at the inland edge of the black prairie belt (described farther on). From the vicinity of Austin southwestward this boundary corresponds pretty closely with a displacement known as the Balcones fault, which marks a rather abrupt transition from the undulating black prairie to the rocky hills of the Edwards Plateau.

As in Alabama, Mississippi and Louisiana, the distribution of vegetation and other biotic features in Texas can be correlated pretty well with geological formations, although there are some discrepancies between existing geological and vegetation maps, which however may diminish with the progress of exploration. But in Texas one encounters an environmental factor that does not occur in the coastal plain anywhere farther east (except to a limited degree on the Florida Keys), namely, aridity. The isohyetal line of 35 inches annual rainfall, which with the temperature prevailing in that latitude marks approximately the transition from humid to semi-arid conditions, passes through or

* A review of this by F. V. Emerson (Geog. Review 2: 384–385. Nov. 1916) reproduces the same map, and may be more accessible to some readers.

near Austin and thence in a southeasterly direction to the Gulf coast.* The trip on which the present paper is based did not take me southwest of Austin, and consequently the following observations are practically confined to the eastern forest region, with ample rainfall.

Previous botanical work in eastern Texas.—The humid portion of Texas (which is approximately the northeastern two thirds of the coastal plain), although it is the most thickly settled and accessible part of the state, has received proportionately much less attention from botanists than the semi-arid portions; presumably mainly because the great majority of the plants there occur also east of the Mississippi River, so that collectors entering Texas from the East have generally pushed on to the drier regions in search of novelties.

This state of affairs is well illustrated by a brief history of botanical investigation in Texas, with a bibliography of about 125 titles, by Charles H. Winkler, constituting University of Texas Bulletin 18 of the 1915 series. Of the works cited therein, 21 are hard to classify or of doubtful value as far as descriptions of the vegetation or flora are concerned, several of them dealing with only one species; 38 relate to Texas and some additional territory besides, chiefly New Mexico or Mexico, or both; 25 cover the whole state, if only for trees or some one family of plants; 34 are restricted to the regions with limited rainfall, and only 7 to eastern Texas alone. If omitted papers (some of which are mentioned farther on) and those published since were added it would not change these proportions much.

Between 1892 and 1896 E. N. Plank contributed to Garden and Forest twenty-nine narratives of botanical trips in Texas (all of which were overlooked by Winkler), but only four or five of these pertain to the humid portions of the state. (In the ten volumes of that magazine there are a few other Texas articles, but apparently none of them touch the area under consideration.)

Professor William L. Bray, while at the University of Texas, sketched the forests of the whole state in 1904 in Bulletin 47 of the U. S. Bureau of Forestry, and again early in 1907 in Bulletin

* See Vernon Bailey's map previously referred to and also the precipitation maps in some of Professor Bray's papers cited farther on.

82 of the University, entitled, "Distribution and adaptation of the vegetation of Texas," using in the latter some of the same half-tone illustrations as in his government bulletin, but including notes on shrubs and herbs as well as trees, more ecological speculations, and an abridged bibliography of twenty titles.

A noteworthy paper on eastern Texas vegetation, not cited by Bray or Winkler, is by the late James E. Gow, on "An ecological study of the Sabine and Neches Valleys, Texas" (Proc. Iowa Acad. Sci. **12**:39–47. *pl. 9–11.* 1905). This divides the vegetation of the area treated (which was mainly in the long-leaf pine region) into six habitat groups, and lists the common trees and a few other plants in each. About the same time appeared U. S. Forest Service Bulletin 64, on "Loblolly pine in eastern Texas," by Raphael Zon, which maps one of the other regions discussed herein and describes the condition of its forests in considerable detail from the standpoint of the professional forester.

J. H. Foster, while state forester, published in 1917, jointly with his assistant H. B. Krausz and one or two others, two useful illustrated bulletins: No. 3, "A general survey of Texas woodlands," and No. 5, "Forest resources of eastern Texas." The first contains a small but pretty good soil map of the state, by a local specialist, and a small map of the forest regions of the coastal plain portion, which fits geographical conditions better in some respects than the maps prepared by geologists and soil investigators.

One of the few "local floras" for eastern Texas is "A list of trees and shrubs occurring in the vicinity of Huntsville, Texas," by Carl Hartman (Trans. Texas Acad. Sci. **12**[2]: 66–90. 1913). This is an annotated catalogue of 62 trees, 24 shrubs, 18 woody vines and two herbaceous vines, but includes 25 introduced or cultivated species, and a few of the shrubs seem to be wrongly identified. An interesting feature of the list is that nearly all the species range far to the eastward, but many of them not much farther westward, showing that the locality is near the western edge of the humid area.

Investigations of the writer.—In July, 1915, I crossed Texas from east to west where it is widest, but on one of the fastest trains, with little opportunity to study any of the vegetation at close

range, and many of the characteristic plants were then unfamiliar to me. In the summer of 1918 a trip through the coastal plain from Virginia to Texas, for the purpose of collecting *Ilex vomitoria* from representative localities for the U. S. Department of Agriculture,* gave me a long-desired opportunity to investigate some of the interesting phytogeographical problems of the "Lone Star State." On this trip I spent a week in Texas, taking notes on the vegetation of at least twenty counties, and walking around in the forests and prairies of four or five of them, where I could thus make more accurate guesses as to the identity of unfamiliar species than was possible from a train. On account of the large territory to be covered in a short time it was not practicable to carry any sort of manual with me or to collect miscellaneous specimens for subsequent identification, but Professor Bray had given me some useful information by letter before I started, and at the University of Texas Miss M. S. Young (since deceased), of the Department of Botany, helped identify a few of the plants that I described to her as having seen a few days before.

My itinerary in Texas in August, 1918, was as follows:

On the afternoon of the 20th I entered the state near the southeastern corner of Newton County by way of the New Orleans, Texas & Mexico Ry. (Gulf Coast Lines)—which comes into Texas on the Kansas City Southern tracks—and stopped at Beaumont, about 25 miles farther on. On the 21st from Beaumont to Port Arthur (about 20 miles) by trolley car, and back the same way except for getting off and walking a few miles through the coast prairies, from Neches Junction to Nederland. On the 22d from Beaumont to Kountze, 25 miles northwestward, by the Texas & New Orleans R. R. (Southern Pacific system), and after exploring the long-leaf pine forests around Kountze for a few hours I went westward by the Gulf, Colorado & Santa Fe Ry., getting well into Montgomery County by nightfall, changing to the H. & T. C. at Navasota, and arriving at College Station about midnight. On the 23d from College Station to Valley Junction and Austin by the International & Great Northern Ry. The 24th

* For an account of some of the results of the trip, see F. B. Power and V. K. Chestnut, *Ilex vomitoria* as a native source of caffeine. Jour. Am. Chemical Soc. 41: 1307–1312. Aug., 1919.

was spent in the vicinity of Austin, part of the time outside of the coastal plain.

On the 25th I went from Austin to Hempstead and Houston, by the Houston & Texas Central R. R. (Southern Pacific). On the 26th from Houston to Columbia by the I. & G. N. Ry., 50 miles, then on foot down the right side of the Brazos River eight or ten miles, to Brazoria, and back to Houston by the St. Louis, Brownsville & Mexico Ry. (Gulf Coast Lines), which uses the Santa Fe tracks the last 28 miles or so. On the 27th from Houston to the Sabine River at Logansport, Louisiana, by the Houston East & West Texas Ry. (Southern Pacific), and on northeastward into Louisiana.

Seven or eight regions were studied sufficiently to be described briefly in this paper, but of course I did not cross their boundaries at enough points to warrant any attempt to revise the regional maps already referred to. The small map published here (FIG. 1) will help the reader to follow the regional descriptions, but in itself can not be regarded as contributing anything new to the knowledge of Texas geography. Two or three of the regions crossed will require further study before they can be described, and for one of them (which may be divisible into two or more) I have not even found a suitable name.*

Observations in the vicinity of Austin.—Near Austin, the only place where I crossed the boundary of the coastal plain in Texas, there is a great contrast between the rocky and almost uninhabited Edwards Plateau west of the city and the undulating and highly cultivated black prairie to the eastward. On the limestone hills I found myself in dwarf forests or thickets as strange to me as were the tropical hammocks south of Miami, Florida, when I first encountered them in the spring of 1909.† This vegetation has been described at considerable length by Professor Bray in some of his best-known papers, and I can add no facts of importance about it. No doubt some of the characteristic species can

* This difficulty is much like that of a taxonomist who monographs a genus or family and finds a few specimens that cannot be referred to known species but cannot be described for lack of information about some of their essential characters.

† In this connection see the chapter entitled "Bewilderment" (pp. 96–103) in Bradford Torrey's book "Nature's Invitation" (Boston, 1904), which describes the author's first experience with the subtropical flora near Miami.

be found at isolated stations farther east (though I have looked in vain in the botanical literature for any definite information on that point), but for all practical purposes the ranges of many must terminate right there.

There is one plant of that neighborhood which deserves special mention here, however. From Palm Valley to Austin, some twenty miles, the International & Great Northern Ry. runs practically on the fall-line, and along there, as well as in a few other

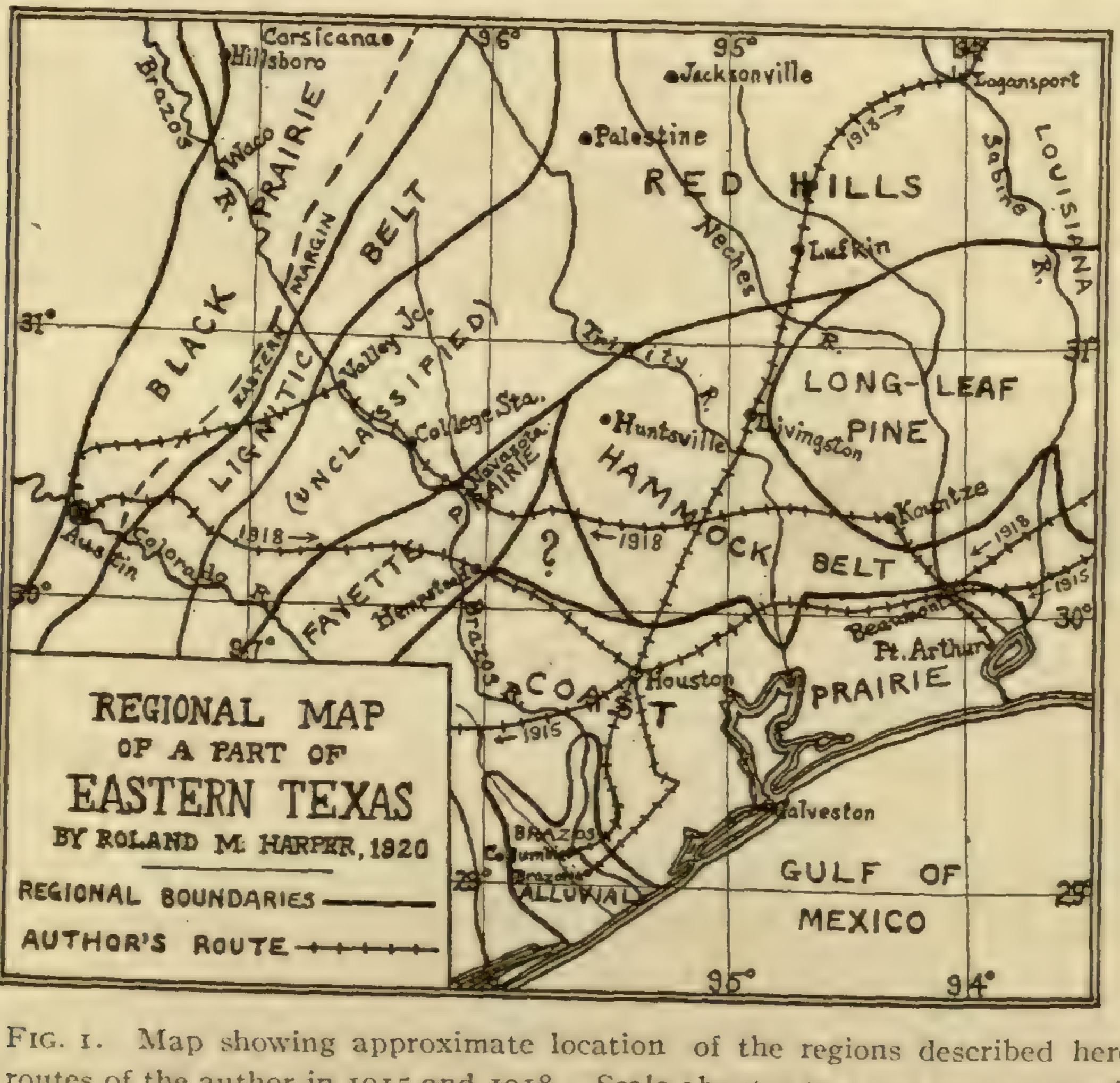

FIG. 1. Map showing approximate location of the regions described herein and routes of the author in 1915 and 1918. Scale about 1 to 4,700,000, or 75 miles to the inch.

places near Austin, a small species of *Tillandsia* was conspicuous on the branches of live oaks. By Texas botanists this has been referred without question to *T. recurvata* L., but it differs from that species as represented in Florida in being more densely tufted, and especially in its environment. It has been made the subject of a special study by Willie I. Birge,* with a map of its

* The anatomy and some biological [*sic*] aspects of the "ball moss," *Tillandsia recurvata* L. Univ. Texas Bull. 194. 24 pp., 10 pls. "Aug. 8, 1911." (Apparently published about the beginning of 1912.)

known distribution in Texas, showing that it extends north to about latitude 31° in Bell County, but no farther east than Fayette and Lavaca Counties, being thus practically confined to the semi-arid regions.* The corresponding plant in Florida is confined to the peninsula, mainly south of latitude 30°, where the average annual rainfall exceeds 50 inches. (There it often grows on insulated wires, which perhaps it does not do in Texas.) The Texas plant at its northern limit must be subject to much colder winter weather than the Florida one, too. If it was all one species there would be no good reason apparently why it should not be found also in Louisiana, Mississippi and Alabama, like *T. usneoides*, with which it is often intimately associated. This seems to be a good opportunity for some taxonomist to investigate and make a new species or subspecies.

REGIONAL DESCRIPTIONS OF THE COASTAL PLAIN

The various divisions of the coastal plain, whose vegetation was studied from the train, will now be taken up as nearly as possible in geological order, beginning at the fall-line and ending at the coast. As usual the plants listed will be divided into trees, shrubs, herbs, etc., and arranged in approximate order of abundance in each group, with the rarer species omitted. The names of evergreens (or in the case of semi-evergreens only the specific names) are printed in heavy type, to suggest the winter aspect of the forests, and those of weeds enclosed in parentheses, so that the reader who may wish to picture to himself the appearance of the original vegetation can skip them.

The black prairie belt is one of the most distinct natural regions in Texas, and it has been delineated pretty accurately on quite a number of maps, geological and otherwise. It corresponds with the area of outcropping of certain upper Cretaceous limestones, plus a strip, a few miles wide at the eastern edge, of the lowest Eocene strata (Midway formation), which is equally calcareous and has very similar soils except for being perhaps a little more rocky. (This strip has been designated by Hill and Deussen as

* This is commented on by Miss Birge on page 8 of her paper as follows: "It is quite evident that *Tillandsia recurvata* demands a semi-arid rather than a swampy environment to which Small in his *Flora of the Southeastern United States* entirely confines it."

the eastern marginal prairie.) The topography is undulating to moderately hilly, and the prevailing color of the upland soils is black or very dark gray. The soil is so fertile that the greater part of the area is cultivated now,* but from all accounts it must have been originally a typical prairie, for there seems to be no record of any forest except along streams and in rocky places.

Many geographical details about this region, with occasional references to vegetation, can be found in Hill's monograph on the Black and Grand Prairies and Deussen's Water Supply Paper 335 previously cited. Published botanical information is rather meager, the writer having found nothing better in that line than a list of a few of the characteristic plants published by Pammel in 1893,† and another short list in Bray's Bulletin 82.

The species observed most frequently from the train, between the eastern edge of Williamson County and Palm Valley, and between Austin and the eastern corner of Travis County, in August, 1918, were as follows:

SMALL TREES

Prosopis glandulosa
Ulmus crassifolia
Hicoria Pecan
Salis longifolia?

SHRUBS AND VINES

Opuntia Engelmanni
Aloysia ligustrina?
Vitis cinerea

HERBS

(*Euphorbia marginata*)
(*Ambrosia trifida*)
(*Helianthus annuus*)
(*Xanthium* sp.)
(*Sorghum halapense*)
Petalostemon sp.
(*Tribulus terrestris?*)

Few if any of these are typical of the original vegetation of the black prairies, for the trees and shrubs are chiefly confined to rocky places, and the herbs are nearly all weeds. Most of the herbs were pretty well dried up (like the corn mentioned a little farther on), but in a wetter season doubtless more species could have been recognized.

* Over 60 per cent of the area of the black prairie counties was classed as "improved land in farms" in 1910, and along my route, in Williamson and Travis Counties, the proportion must be above the average, for I would have guessed it to be something like 90 per cent.

† Proc. Iowa Acad. Sci. 1[3]: 62. 1893.

This region has been correlated by geologists and soil investigators with a well-known belt of similar age in Mississippi and Alabama, but it differs widely from that in some features of soil, vegetation, population and agriculture. In the eastern black belt the black soils are limited in extent and chiefly confined to low grounds, while in the Texas area black is the prevailing color even on the uplands. The eastern belt has most of its rain in winter and spring, and the western in early summer. The originally treeless areas probably did not cover more than 10 per cent of the black belt in Alabama and Mississippi, while the Texas black belt must have been nearly all prairie. In the black belt of Alabama about three-fourths of the inhabitants are negroes (which has led some persons in other states to imagine that its name referred to that fact), while in the corresponding part of Texas negroes constitute only about one sixth of the total.

In the last ten years or so, since the coming of the boll-weevil, the cotton fields of central Alabama have largely given way to hay and pasture; but in the black belt of Texas, which has had the weevil much longer, cotton is still king, and there is very little pasture, at least in the latitude of Austin. In 1909–1910 the average farm in that region had about 32 acres of cotton and 15 of corn out of a total of 64.5 "improved," and the yield of both was above the state average. At the time of my last visit the precipitation had been below normal for several months over most of Texas, and the corn-stalks standing in the fields, from which the "fodder" had been "pulled" some time before, were bleached to a pale straw color, contrasting strongly with the black soil; while the cotton in neighboring fields, though short of stature, was full of healthy dark green leaves: and I do not remember ever seeing paler corn or greener cotton plants.

In this region I was impressed with the neat and prosperous appearance of the farm-houses, which appeared almost equal to those of Illinois. On digging out statistics later from census reports I found that the average value of farm buildings in 1910 in 15 black prairie counties of Texas was only $592 ($641 for whites*

* If we had figures for Anglo-Saxons alone the building values for that race would be higher than those given above, for the white population of this part of Texas includes quite a number of Mexicans (not separated in the census unless they happened

and $241 for negroes), which seems rather low; but the two counties that I crossed are above the regional average in that respect, and there may also have been some improvement between 1910 and 1918. Windmills, another token of moderate prosperity, are much more frequent in the black prairie belt than in the regions farther east.

The Lignitic belt.—At the eastern edge of the black prairies as above defined there is a pretty sudden transition to a non-calcareous belt, about 15 miles wide in the latitude of Austin but wider northward, characterized by Eocene strata of the Wilcox formation (Lignitic of the older geologists), which give rise to rather sandy soils with pale clayey subsoils. There is also a good deal of ferruginous sandstone, similar to that which can be seen on many non-calcareous uplands in the coastal plain from New Jersey to Mississippi. Quite a number of lignite mines and brick and tile plants can be seen from the train, and the domestic water supply is mostly from dug wells, indicating pretty good water—something that is not very abundant in Texas. On account of the comparatively poor soil, only about one fourth of the area is cultivated (30.5 per cent improved in 1910 in a few selected counties, all of which include parts of more fertile regions on either side).

I crossed this belt in 1915 in Caldwell and neighboring counties, and in 1918 in Milam and Bastrop, but only the 1918 notes are used here. The vegetation has little in common with that of the black prairies. *Quercus stellata* constitutes about two-thirds of the forest and *Q. marylandica* about one third, and both are small, hardly fit for saw timber. No regular shrubs were noticed, but *Vitis cinerea* is a common vine, and *Daubentonia longifolia* (called *Sesbania Cavanillesii* by some of the older writers on Texas plants, such as Plank), a tall woody herb or short-lived shrub, is a common weed. The prevailing herbs are about as follows:

Andropogon scoparius
(*Croton capitatus*)
Eupatorium compositifolium
(*Helenium tenuifolium*)
(*Sesbania* sp.?)
Baptisia leucophaea?
(*Froelichia campestris*)

to be born in Mexico, though some of the counties provide separate schools for them as they do for negroes), and their standards of living are little if any higher than those of the negroes. In the Alabama black belt the average farm building values for whites and negroes in 1910 were $897 and $114, respectively.

An interesting feature of this belt is the occurrence, in its northern portions, of several "salt domes," which have attracted considerable attention from oil prospectors but which have apparently never been investigated botanically.*

An indication of the difference in soil fertility between this and the black prairie belt is that in 1909–10 the prairie farmers spent less than a third of a cent for fertilizers, for each acre of improved land, while those in the Lignitic belt spent a little over two cents an acre.

Areas of uncertain relationship.—East of the Lignitic belt and west of the Trinity River are the Fayette prairie and one or two other kinds of country that have not been accurately mapped, and whose boundaries I could not locate satisfactorily in the short time available, especially when I crossed some of them at night. The belt in which College Station is situated seems to be characterized by buff-colored rather clayey soils of medium fertility, and very open forests of small oaks and other deciduous trees. The Fayette prairie resembles the black prairie in the color of its soil, but is flatter and less than half cultivated, with a larger percentage of negroes. Live oak growing in clumps or "motts" is a characteristic feature in some places. The yield of corn per acre, in a few counties selected as typical, is even higher than in the black prairie. The blackness of the soil is noteworthy, for it is derived from Eocene strata that are not as obviously calcareous as are the Cretaceous rocks of the black prairie. For some reason apparently not yet explained, almost any formation in Texas can make a black soil, just as in Alabama and Georgia many kinds of rock weather into red clay, and in Florida the final product is commonly sand. In some parts of eastern Texas one can see the curious combination of black soils and red subsoils. No doubt the complete explanation will have to take climate into consideration.

The red hills, or short leaf pine region.—This region, in the extreme eastern part of the state, is an extensive area characterized by Eocene strata a little younger than those of the Lignitic belt,

* For a description of one about a mile in diameter, in Freestone County, surrounded by a narrow strip of marsh grass, see E. DeGolyer, Jour. Geology (Chicago) 27: 647–663. *f. 1, 2.* "Nov.–Dec. 1919" [Feb. 1920].

which adjoins it on the west. The boundary between this and the nondescript country around College Station has not been definitely located, but is probably somewhere near the Trinity River. This region does not differ conspicuously from the Eocene red hill belt that extends from South Carolina to Mississippi, but it is separated from that by the width of the Mississippi River bottoms, a gap of about 100 miles.*

FIG. 2. Looking south from train at Hanson, Shelby County, about six miles from the Sabine River; a scene very typical of the red hill region as far as topography, general aspect of forests, and relative amount of cleared land is concerned. August 27.

The soil is usually reddish and loamy, the topography moderately hilly (see FIG. 2), and the country about one third cultivated. In 1909–10 about two thirds of the farmers were white, 28 per cent of the land "improved," and the average expenditure for fertilizers 13 cents an acre. The average yield of corn was about 13 bushels per acre, as in the Lignitic belt.

There seems to be very little information about this part of Texas in the botanical literature. Plank's "Botanical notes from

*For descriptions of portions of this belt east of the Mississippi, see Bull. Torrey Club 37: 411. 1910; 40: 386–388. 1913.

Texas, XXIV"* deals with Cherokee County, but mentions only about a dozen species of plants, and several of these are introduced. I crossed the region in going from Houston to Shreveport, and the country between Lufkin and the Sabine River (72 miles) may be considered typical. The following seem to be the commonest woody plants along the route just indicated.

LARGE TREES

Pinus echinata
Pinus Taeda
Quercus falcata
Liquidambar Styraciflua
Quercus stellata
Quercus marylandica
Hicoria alba
Quercus Phellos
Ulmus americana
Quercus alba
Quercus **nigra**
Nyssa sylvatica?

SMALL TREES

Salix nigra?
Morus rubra
Cornus florida
Cercis canadensis
Carpinus caroliniana
Magnolia glauca
Crataegus berberifolia?

SHRUBS AND VINES

Brunnichia cirrhosa
Rhus glabra
(Daubentonia longifolia)

As in many other wooded regions, the herbs recognizable from a train in summer are mostly weeds. *Helenium tenuifolium* seems to be the most abundant and *Croton capitatus* next, and the others are considerably scarcer.

The long-leaf pine region.—This lies south of the red hills, but not necessarily immediately adjacent thereto. (Not having passed directly from one to the other in Texas, I cannot say whether the transition is abrupt or there is some other kind of country between, as the geological maps suggest.) Its western limit seems to be in Polk County, though very likely there are scattered long-leaf pines outside the area indicated on the map. It does not correspond with any one formation on the latest geological maps, but its strata are approximately contemporaneous with the Altahama Grit of Georgia and probably not older than Miocene. The topography of the parts I saw is gently undulating, but it is said to be more hilly farther north. Running water is rather scarce, probably on account of the soil, which instead of being decidedly sandy and holding water long after a rain, as in the Atlantic pine

* Garden & Forest 8: 72–73. Feb. 20, 1895.

forests, is usually a pale yellowish loam. The Neches River, which drains a large part of this region, seems to be less muddy than most other Texas rivers, however.

The government soil survey of the "Woodville area," made in 1903, describes an area ten miles square in Tyler County. There are notes on the pine timber in several papers on forestry, but previous descriptions of the vegetation as a whole are not very satisfactory. The scene of Plank's first Texas article, in Garden and Forest (5: 399) for August 24, 1892, is laid in Tyler County, but there is no mention in it of the characteristic herbs of the pine forests, or even of *Pinus palustris*, for that matter (which may indicate the presence of considerable areas of hardwood forest in the heart of the long-leaf pine region). Gow, in the paper already cited, listed 11 woody plants and 10 herbs as characteristic of long-leaf pine flats in winter and early spring, and two additional trees from pine uplands. Bray sketched the herbaceous vegetation briefly, on pages 84–85 of his University of Texas Bulletin 82, but listed only four or five species, and regretted his unfamiliarity with that part of the state.

Although the soil if seen without its vegetative covering would look pretty good, it is evidently below the average in fertility, as is the case nearly everywhere where *Pinus palustris* abounds. Improved land constituted less than 4 per cent of the total area in 1910, and the few farmers that cultivated it were then spending about 30 cents an acre for fertilizers, which is probably more than in any other equal area in the United States west of the 93d meridian. Over 70 per cent of the farmers were white, their farms averaged about 25 acres of improved land each (probably the smallest in Texas outside of irrigated districts), of which about three acres were devoted to cotton and ten to corn, and the yield of corn was about 15 bushels per acre.

My observations on this region in Texas were limited to near its southern edge, in Hardin County. As in near-by parts of Louisiana, *Pinus palustris* is practically the only tree on the uplands there, but the small dry waterways are bordered by strips of hammock-like vegetation, which might be regarded as extensions or prongs of the region next to be described. The following list is based on my walks around Kountze, the county-seat, on August

22, extending not more than two miles east, north and west of there, and a few miles of car-window notes southeast and west of the same place. Plants of all habitats, including weeds, are combined here, as in the preceding lists.

LARGE TREES

Pinus palustris
Pinus Taeda
Magnolia grandiflora
Liquidambar Styraciflua
Quercus alba
Quercus falcata
Fagus grandifolia
Nyssa biflora?
Quercus laurifolia
Quercus Michauxii
Hicoria alba

SMALL TREES

Magnolia glauca
Cornus florida
Ilex opaca

LARGE SHRUBS

Ilex vomitoria
Myrica cerifera
Cyrilla **racemiflora**
Liquidambar Styraciflua
Cephalanthus occidentalis
Callicarpa americana
Batodendron **arboreum**
Symplocos **tinctoria**

SMALL SHRUBS

Myrica pumila
Hypericum aspalathoides?
Ascyrum stans
Magnolia glauca
Rhus Toxicodendron

FIG. 3. Virgin forest of long-leaf pine, with no other woody plants in sight about two miles northwest of Kountze, Hardin County. August 22.

HERBS

Andropogon furcatus?
Laciniaria acidota
Laciniaria pycnostachya?
(*Diodia teres*)
Chamaecrista fasciculata
Eupatorium rotundifolium
Chrysopsis graminifolia
Boltonia diffusa
Pluchea foetida
Solidago odora
Solidago nitida?
Cracca spicata?
Eupatorium Mohrii?
Linum floridanum?
Eupatorium tortifolium?
Rhexia mariana?
Euphorbia corollata
(*Helenium tenuifolium*)
Mesosphaerum rugosum
Diodia virginiana
(*Euphorbia maculata**)
Rudbeckia hirta?
Polygala mariana?
Helianthus angustifolius
Eupatorium semiserratum?
Chondrophora nudata
Marshallia graminifolia
Eryngium ludovicianum
Nama corymbosum
Baptisia leucophaea?
Stylosanthes biflora
Ruellia humilis

(and about 20 others)

All the trees except the first-named and also the large shrubs are chiefly confined to the hammocks, and most of the other species to the open pine forests, where they are subject to periodical fires, as in all other forests of long-leaf pine that I have seen. The scarcity of woody vines here, as in the eastern pine-barrens, is probably correlated with fire. The first herb listed is probably more abundant than all the others combined, but as it was not in bloom at the time, I could not be sure of the species.

A peculiar feature of the shrubby and herbaceous vegetation of the open pine forests is that some species which in Georgia and Alabama are chiefly confined to damp spots and others which are usually regarded as pronounced "xerophytes" here associate together either in hollows or on the highest spots; possibly because both situations become about equally dry in dry seasons. The only *Sarracenia* known in Texas, *S. Sledgei*, has been reported from (near?) Kountze by Professor Macfarlane† (who first distinguished it from *S. flava*), but I did not come across any place wet enough for it.

* Although one finds no statement to that effect in any of the manuals, the favorite habitat of this species seems to be railroad tracks. I have seen it in such situations in places as far apart as Massachusetts, Michigan, Florida and Texas.

† Engler's Pflanzenreich 4^{110}: 29. 1908. See also Jour. Elisha Mitchell Sci. Soc. **34**, 119. 1918. (No proof of this last was sent to me, and consequently it contains several annoying typographical errors, most of which however are self-evident.)

My lack of books and collecting apparatus on this trip is reflected in the large number of interrogation points in the foregoing list, which however is probably the most complete hitherto published for this region. If there had been any descriptions of pine-barren vegetation in either Texas or western Louisiana to go by it would have facilitated the identification of the species, but previous botanical explorers of this region seem to have either visited it in winter, or concentrated their attention chiefly on the trees, or merely collected plants without trying to describe the vegetation. The great majority of the species identified grow also east of the Mississippi River, where there are scores of pine-barren plants that do not reach Texas. Consequently the Texas pine-barren flora is much less attractive to taxonomists than that farther east, which probably explains why so little has been written about it.

The hammock belt, or Pinus Taeda region.—The long-leaf pine region is bordered on the south and west by a belt of varying width containing what are probably the densest upland forests in Texas,* in which *Pinus Taeda* is more abundant than any other tree, and than it is in any other equal area west of the Mississippi River, apparently. This belt or region, which extends across two or three geological formations without much change, has been mapped pretty well by Zon in Bulletin 64 of the U. S. Forest Service, and by Foster and Krausz in their State Forester's Bulletins 3 and 5, previously mentioned. The boundary between this and the long-leaf pine region is very sharp where I crossed it, about twelve miles southeast and west of Kountze, even if it may be less sharp at other points. There does not seem to be any marked difference in topography, and the change can hardly be correlated with geology, but there must be a considerable difference in soil fertility.

In 1909–10 about 10 per cent of the area was classed as improved land (over twice as much as in the long-leaf pine region), and the farmers spent about 7 cents an acre for fertilizers, which is above the Texas average but less than a third as much as in the long-leaf pine region. Nearly half the farmers were negroes, and

* The term "Big Thicket" is said to be applied locally to part of this region, in Hardin and Liberty Counties.

this is probably not the most salubrious region in the state, particularly along the Trinity River, where there is an alluvial belt a few miles wide so fertile that few pines are to be seen. (The Trinity drains a considerable portion of the black prairie previously described, and must carry down a great deal of fertility to be deposited farther along its course.) The average value of farm buildings is lower than in any of the other regions here discussed, being, in 1910, $325 for whites and $123 for negroes.

My notes on the hammock belt happen to be more complete than for any of the other regions that I saw only from the train. I was in it from the Sabine River to Beaumont and about ten miles northwest thereof, and then from about twelve miles west of Kountze to a point in Montgomery County undetermined on account of darkness, and a few days later from about Humble to Livingston; giving about 125 miles of car-window notes in all. (On the 22nd I must have passed out of it soon after nightfall, probably about Conroe, for I could see by the light of the full moon that the country west of that point was more open than that to the eastward. Notes taken north of Livingston on the 27th have not been counted in the following list, for beyond that point I was too close to the edge of the region to see a typical section of it.)

The list of plants is as follows; and in reading it it will be well to bear in mind that the first tree listed seems to be several times as abundant as its nearest competitor, though it may not constitute as much as half of the forest.

LARGE TREES

Pinus Taeda
Liquidambar Styraciflua
Pinus echinata
*Nyssa biflora?**
Magnolia grandiflora
Quercus Phellos
Quercus falcata
Quercus alba
Quercus Michauxii
Quercus **nigra**
Pinus palustris
Quercus stellata
Hicoria alba
Quercus laurifolia
Hicoria Pecan?
Quercus hybrida?
Taxodium distichum
Platanus occidentalis
Nyssa uniflora
Ulmus alata
Quercus pagodaefolia?

* In Florida *Nyssa biflora* seems to be a perfectly distinct species, but near its northern and western limits it is sometimes hard to distinguish from *N. sylvatica*.

SMALL TREES

Salix nigra?
Ostrya virginiana
Planera aquatica
Ilex opaca
Cornus florida
Magnolia glauca

SHRUBS AND VINES

Ilex vomitoria
Sabal glabra
Callicarpa americana
Rhus copallina
Myrica cerifera
(Daubentonia longifolia)
Vitis rotundifolia

HERBS

(Helenium tenuifolium)
(Croton capitatus)
Tillandsia usneoides
Eupatorium compositifolium?
(Euphorbia marginata)

It seems probable that this region has more species of timber trees than any other reasonably homogeneous area of the same size in Texas.* Nearly all of them are equally common as far east as Georgia—and most of them extend even to Maryland—but *Magnolia grandiflora* seems to be a little more abundant here than it is anywhere east of the Mississippi River. The abundance of *Ilex vomitoria* is rather surprising, for east of New Orleans its favorite habitat is sandy hammocks within a mile of salt water. The proportion of evergreens is pretty high, for Texas, presumably indicating soils below the average in fertility, though not the poorest in the state.

The coast prairie.—On the south, not far from the main line of the Texas & New Orleans R. R. (Southern Pacific) from Orange to Houston, the hammock belt passes gradually into the coast prairie, an extensive and interesting region which has never been adequately described botanically. There are some outlying bodies of pine in the prairies, and some isolated prairies within the edge of the timber belt; and the opinion has been expressed by competent observers that the forest is encroaching on the prairie, rather rapidly for a successional change. The prairie region extends inland nearly to Hempstead,† in Waller County, 100 miles

* Hartman, in the paper cited on a preceding page, enumerates 43 native species of trees from the vicinity of Huntsville.

† Very likely this name was derived indirectly from Hampstead Heath in England, like that of Hempstead, Long Island, which is in the only known prairie east of the Alleghanies, and Hempstead County, Arkansas, which contains a few areas of black prairie similar geologically to that in Texas.

from the coast and about 250 feet above sea-level. Generally speaking, it is a vast flat plain, diversified in many places by mounds about a foot high and a few yards wide and depressions or "hog-wallows" that are even flatter, and less frequently by shallow waterways and a few "domes" that are of about the same shape as the mounds but many times larger.*

Where the coast prairie extends farthest inland the soil is a sort of sandy loam, dry enough in places to afford a suitable habitat for a *Selaginella* of the *rupestris* group;† but toward the coast, with decreasing altitude, and also with heavier summer rain (which naturally counterbalances the evaporation more than the same amount in winter would‡), the surface becomes more and more marshy, and at the same time more clayey, though the reason for this is not quite so obvious. In color the soil varies from gray to brown and nearly black, and it must be quite fertile, though the tests of evergreen percentages and amount of improved land, which have been used for some of the foregoing regions, are hardly applicable.

The greater part of the area has never been cultivated (in 1910 only about 40 per cent of it was in farms and 14 per cent improved), but there is a surprisingly large number of weeds, perhaps attributable to over-grazing, although very few cattle were in evidence at the time of my visit. It is very difficult, for a newcomer at least, to tell just which species are weeds and which are natives, so that the number of parentheses in the following list should not be taken too literally.

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* For topographic maps of parts of the coast prairie in Harris County, on a scale of two inches to the mile, with one-foot contour intervals, see the Cypress, Addicks and Aldine quadrangles of the U. S. Geological Survey, published in 1918 and 1919. The narrow wooded areas along streams are indicated by green overprint.

The cause of the prairie mounds is still a mystery (see Plant World 17: 39, 41. 1914), but the domes are geological structures, which usually indicate accumulations of salt or petroleum, or both. The most noted dome in the whole country is Spindletop, a few miles south of Beaumont. Oil derricks are abundant there and in numerous other places scattered over the prairie coast.

† The type specimen of *S. Riddellii* Van Eseltine (Contr. U. S. Nat. Herb. 20: 162–163. Nov. 1918) is from Prairie View, Waller County.

‡ See Science II. 48: 208–211. Aug. 30, 1918. At Port Arthur, in the southeastern corner of the state, every house has a galvanized iron cistern to catch water from the roof, indicating copious summer rain and—presumably—unpalatable ground-water.

One might suppose that such a large and interesting and easily accessible prairie area would long ago have attracted both taxonomists and ecologists in considerable numbers, and that several descriptions of it would have been published before this: but the information about it in the existing botanical literature is so meager* as to be of very little assistance in identifying the plants that were not in bloom the latter part of August. Consequently the subjoined list contains many interrogation points, and even the names not queried should not be accepted without reservations; but this is at least superior to previous lists for the same region in being longer and having the species arranged in approximate order of abundance.

The composition of the prairie vegetation varies considerably from place to place, even where soil conditions appear to be the same, and—which cannot be said of the three regions last described—many of the species are unknown east of the Mississippi River. This, together with the lack of flowers in many cases (which made even generic identifications doubtful sometimes), made it impossible for me to get a thoroughly representative list of plants in the short time available.

Trees in the coast prairie are chiefly hardwoods characteristic of the neighboring hammock belt, growing on the banks of permanent or intermittent streams, small groves of *Pinus Taeda* near the inland edge, and a species of *Crataegus* near the Brazos alluvial region to be described next. The only native shrubs observed were *Myrica pumila*, which is common on mounds and in other dry places, and *Borrichia frutescens*, in damp spots toward the coast.† If the exotic *Daubentonia longifolia* is classed as a shrub (and it is certainly much larger than the two native shrubs just mentioned, though probably shorter-lived), it is the most abundant one at the present time, in all sorts of places. *Rosa bracteata*, an Asiatic species, is scattered around Rosharon, in Brazoria County.

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* A few of the characteristic genera, both native and introduced, are mentioned on pages 19–20 of Bailey's Biological Survey of Texas; and Bray, on page 86 of his Bulletin 82, lists 22 species and 4 additional genera from the coast prairie, apparently mostly spring-flowering.

† Shrubs not provided with subterranean stems, as *Myrica pumila* is, would lead a very precarious existence on a prairie subject to fire.

The following herbs were noted in going from Beaumont to Port Arthur and back (three or four miles of it on foot) on August

FIG. 4. Prairie vegetation south of Nederland, Jefferson County. *Euphorbia marginata* and *Eupatorium serotinum* in foreground. August 21.

22, from Prairie View to Houston on the 25th, and from Houston to Columbia and Brazoria to Houston on the 26th.

(*Euphorbia marginata*)
(*Croton capitatus*)
Euphorbia hexagona?
Gaura Lindheimeri
Mesadenia lanceolata
Chamaecrista fasciculata
Helianthus sp.?*
Baptisia leucophaea
(*Helenium tenuifolium*)
(*Glottidium vesicarium*)
Eryngium yuccifolium
Eupatorium serotinum
Bollonia diffusa
Chaetochloa sp.
Diodia virginiana
(*Capriola Dactylon*)
Centella repanda
Paspalum sp.
Ambrosia psilostachya
Spartina patens?
Lythrum lanceolatum?
Neptunia lutea?
Euthamia lanceolata?
Baptisia sphaerocarpa?
Jussiaea grandiflora
Mimosa strigillosa?
Sarothra Drummondii
(*Euphorbia maculata*)
Spilanthes repens
Cuscuta arvensis
Spartina junciformis?
Eryngium Leavenworthii?
Nama corymbosum
Lippia sp.

(and about 40 others less abundant)

*A small erect composite with roughish linear leaves, not in bloom at this time, so that the genus is uncertain.

No doubt observations made along other routes, at other seasons, and after more experience in this part of the country would greatly extend this list and change the sequence considerably. But it is probably safe to say at this time that the families most largely represented are Compositae, Leguminosae, Euphorbiaceae and Gramineae (using these names in the older and broader sense), and that the total number of native species that could be found is well over 100. The general aspect of the vegetation is much like that of some Illinois prairies, but the flora is of course very different, on account of the difference in climate. There is naturally a little more resemblance to the Grand Prairie of Arkansas.*

A few of the economic features of this region may be of interest, besides the area of farm land which has already been given. In 1910 the foreign white farmers (19 per cent of the total) outnumbered the negro farmers (15 per cent). The average white farmer had 205 acres of land, of which 71 were improved, including 2.7 acres of cotton and 7.9 of corn; and his buildings were worth $842. The yield of corn was 22.2 bushels per acre, which is higher than in any of the regions previously described, and seems to indicate that prairie soils are best for corn. (The black prairie ranked next in this respect.)

The average negro farmer had 70 acres with 28 improved, of which 3.3 were in cotton and 5.7 in corn. His buildings were worth $256 (a little more than in the black prairie), and his corn crop was 16.4 bushels per acre.

The Brazos alluvial region.—All the streams traversing the coast prairie seem to be bordered by strips of woodland, but along the Brazos and one or two near-by rivers near their mouths the wooded area is large enough to be treated as a separate region, as shown on the map. Its boundaries are pretty well defined, on the east at least, and it is said to cover about 900 square miles, mostly in Brazoria County. It has been described by Loughridge in his report on the cotton production of Texas,† and by Wm. T. Carter, Jr., in a "Reconnoissance soil survey of the central Gulf coast area of Texas."‡ The latter covers all of this region except the

* See Plant World **17**: 40–44. 1914; **20**: 58–61. 1917.

† Tenth Census U. S. **5**: 702–704. 1884. This includes two soil analyses.

‡ Field Operations U. S. Bur. Soils **1910**: 859–929. *pl. 1–8.*

small portion in Fort Bend County, as well as several counties occupied chiefly by coast prairie.

This is not exactly a delta, as one might imagine from the map, nor even a flood-plain, for it is not noticeably lower than the adjacent country, and it does not appear to be subject to frequent inundation. At Columbia, about 25 miles from the coast, both banks of the river are something like 30 feet high and rather steep, which is quite a different condition from that along most rivers from New Jersey to Florida at that distance from their mouths, where the banks are usually low and swampy. (The Brazos differs also from most rivers of its size farther east in the coastal plain in having practically no navigation. Although it is about a thousand miles long and is said to have a drainage area of over 40,000 square miles, the highway bridge at Columbia, though equipped with a draw span, had that permanently closed at the time of my visit so that it could not be turned to allow steamers to pass.)

The soil varies with the distance from the river and coast, but much of that which I walked over between Columbia and Brazoria is a chocolate-colored stiff clay, designated on the government soil map just cited as "Trinity clay." A few of the characteristic trees were listed by Loughridge, and Carter described briefly the vegetation of nearly every type of soil in the whole area mapped by him, except—curiously enough—the "Trinity clay," which covers the greater part of the alluvial region. Both Loughridge and Carter make special mention of the "wild peach," *Prunus caroliniana*, and Carter states that it is the most characteristic tree of one of the less extensive types of soil, the "Pledger silt loam," the boundaries of which may be traced by its presence. But strange to say, I did not happen to see any of it, or of *Juniperus virginiana*, which according to Professor Bray* was formerly abundant in this region, at least near the mouth of the San Bernard River.

My observations in this rather unique area were all made on August 26, from the train, for about ten miles before arriving at Columbia, and in walking down the west side of the river, probably nowhere more than a mile from it, to Brazoria, and then from another train from Brazoria a few miles northeastward to the edge of the prairie again. The commonest plants seem to be as follows:

* U. S. Forestry Bull. 47: 54. 1904; Univ. Texas Bull. 92: 68. 1907.

LARGE TREES

Hicoria Pecan — *Acer Negundo*
Quercus virginiana — *Gleditsia triacanthos*
Ulmus crassifolia — *Quercus* **nigra**
Celtis sp.

SMALL TREES

Crataegus sp. — *Salix nigra?*

SHRUBS AND VINES

Ilex vomitoria — *Rhus radicans*
Ampelopsis arborea — *Tecoma radicans*
Sabal glabra — *Ilex decidua*
Vitis cinerea — *Berchemia scandens*

HERBS

Tillandsia usneoides — (*Atheropogon curtipendulus*)
(*Daubentonia longifolia*) — (*Helenium tenuifolium*)
(*Cardiospermum Halicacabum*) — (*Croton capitatus*)
(*Euphorbia marginata*)

The abundance of trees and shrubs with small thick or evergreen leaves—such as *Quercus virginiana*, *Ulmus crassifolia*, *Ilex vomitoria*, and the two trees mentioned in a preceding paragraph—and the absence of *Liquidambar*, in such a rich-looking

FIG. 5. *Ilex vomitoria*, *Hicoria Pecan*, *Sabal glabra*, etc., on dark brown stiff clay in Brazos River bottoms between Columbia and Brazoria. August 26.

soil, is rather surprising. It is also interesting to note that there are more vines than shrubs in the list, and that all the herbs but the first-named (and that is an epiphyte) are weeds. The scarcity of native herbs in a list made up from car-window notes in a densely wooded region would not be surprising, but in this case I was on the ground for a few hours, and walked eight or ten miles. Several other herbs were seen only once or twice and therefore not listed above, but practically all of those were weeds too.

The economic features of this region deserve a passing mention. It covers about half of Brazoria County, and the census statistics for that county therefore give an approximation of conditions in the alluvial region. Less than 10 per cent of the area of the county was cultivated in 1910, and there were nearly as many negro as white farmers. (Negroes are probably in the majority in the alluvial region.) The average white farmer in the county had 240 acres, of which 57 were improved, and buildings worth $917; while the negro farmer got along with 41 acres, 25 of them improved, and buildings worth $165. The large size of the white men's farms and the value of the buildings on them (surpassing any other region in eastern Texas in both respects) probably indicate that many if not most of them were sugar plantations. For according to Loughridge this region was called the "sugar-bowl" of Texas, on account of being the chief sugar-producing area of the state.* The average white farmer in the county had only about 2 acres in cotton and 8 in corn, while his negro neighbor had nearly 7 acres in cotton and 8½ in corn. The yield of cotton in 1909 was very low, only about a tenth of a bale per acre.

CONCLUSION

A week's sojourn in eastern Texas, supplemented by examination of the literature afterward, brought out some very pronounced contrasts between different portions, and considerable difference between the area as a whole and other parts of the coastal plain in the same latitude several hundred miles farther east, say in Alabama and Georgia, where temperature conditions are substantially the same and the annual precipitation not much greater.

* In 1880 the only Texas counties that had more than 300 acres of sugar-cane were Brazoria, with 3358, and Fort Bend, with 1738. In 1910 Fort Bend had 6775 acres, Wharton 4714, and Brazoria 2037. (These three counties are all contiguous.)

Considering physical features first, Texas evidently has more black soil and less sand and red soil, less potable water, water-power and navigation, and fewer gullies, steep hills, rich woods, ravines, caves, springs, clear streams, non-alluvial swamps, and bogs than the more easterly states.

Botanically eastern Texas, comparatively speaking, seems to be poorly provided with shade-loving spring flowers, *Sphagnum*, ferns, *Juniperus*, *Taxodium*, orchids, *Arundinaria*, Cyperaceae, *Populus*, *Betula*, *Alnus*, *Fagus*, *Quercus alba*, *Magnolia glauca*, *Liriodendron*, *Platanus*, *Acer rubrum*, *A. saccharinum*, *Sassafras*, *Cornus*, *Nyssa*, Ericaceae and *Sambucus*, to mention a few of the more obvious cases. If we had more complete information about the composition of Texas soils we could probably explain some of these things better than we can now.

INDEX TO AMERICAN BOTANICAL LITERATURE

1915-1920

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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Arber, A. Leaf-base phyllodes among the Liliaceae. Bot. Gaz. **69**: 337–340. *f. 1–4.* 16 Ap 1920.

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Benoist, R. Description d'espèces nouvelles de Phanérogames de la Guyane française. Bull. Mus. d'Hist. Nat. (Paris) **1919**: 296–299. Ap 1919.

Capparis maroniensis, Andira Wachenheimi, Swartzia similis, and *Helicostylis pedunculata* are enumerated.

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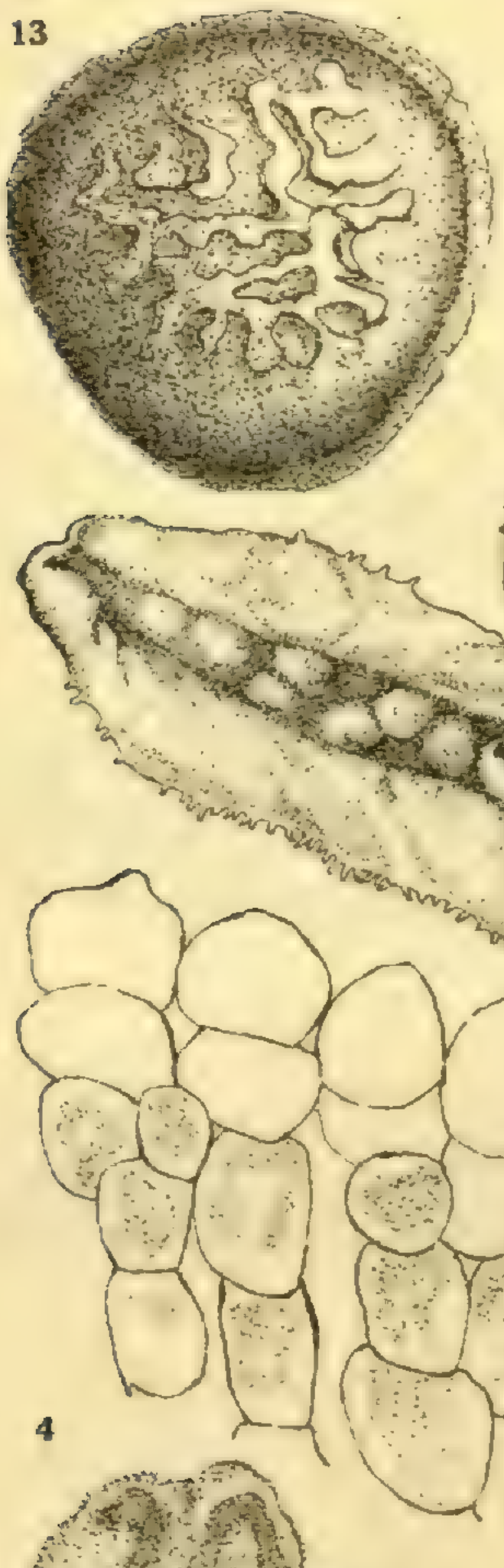
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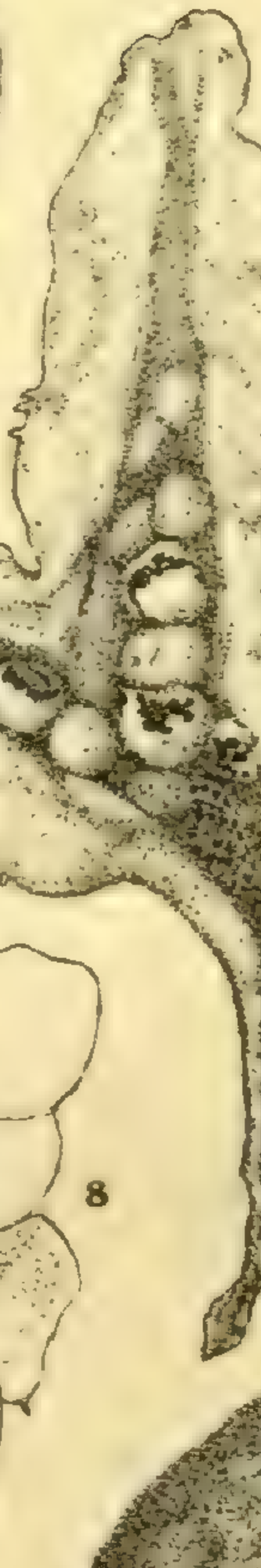
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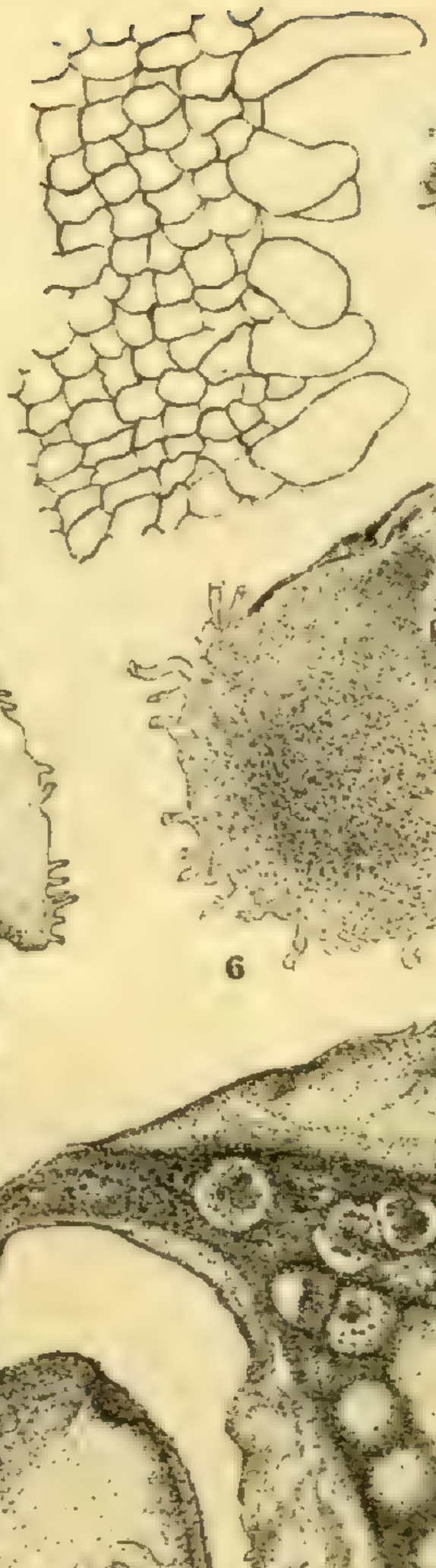
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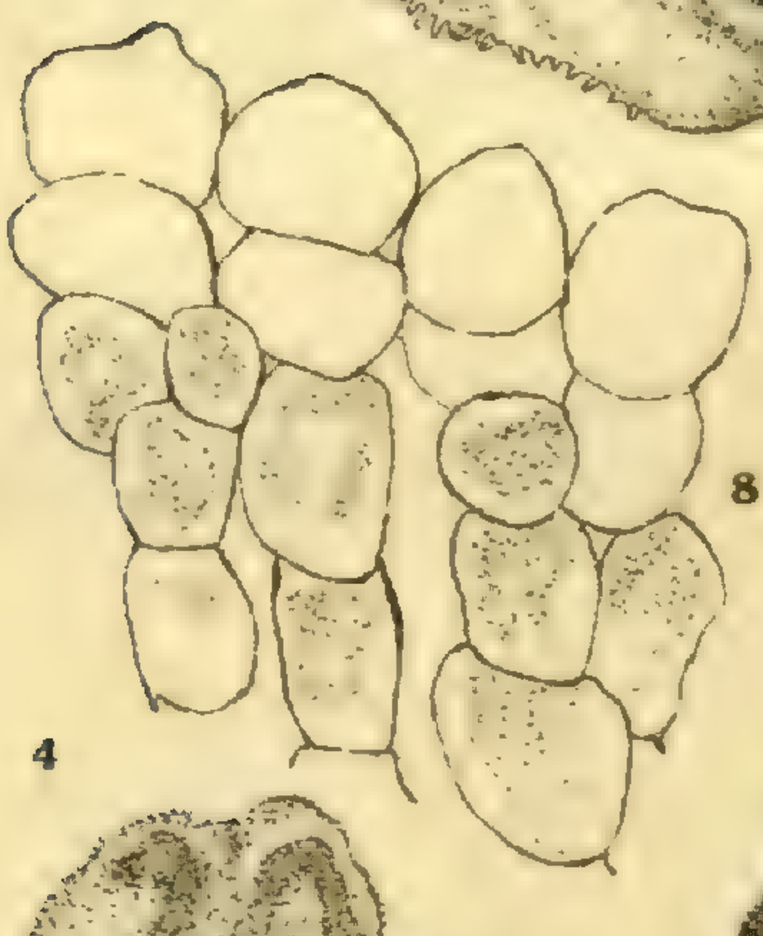
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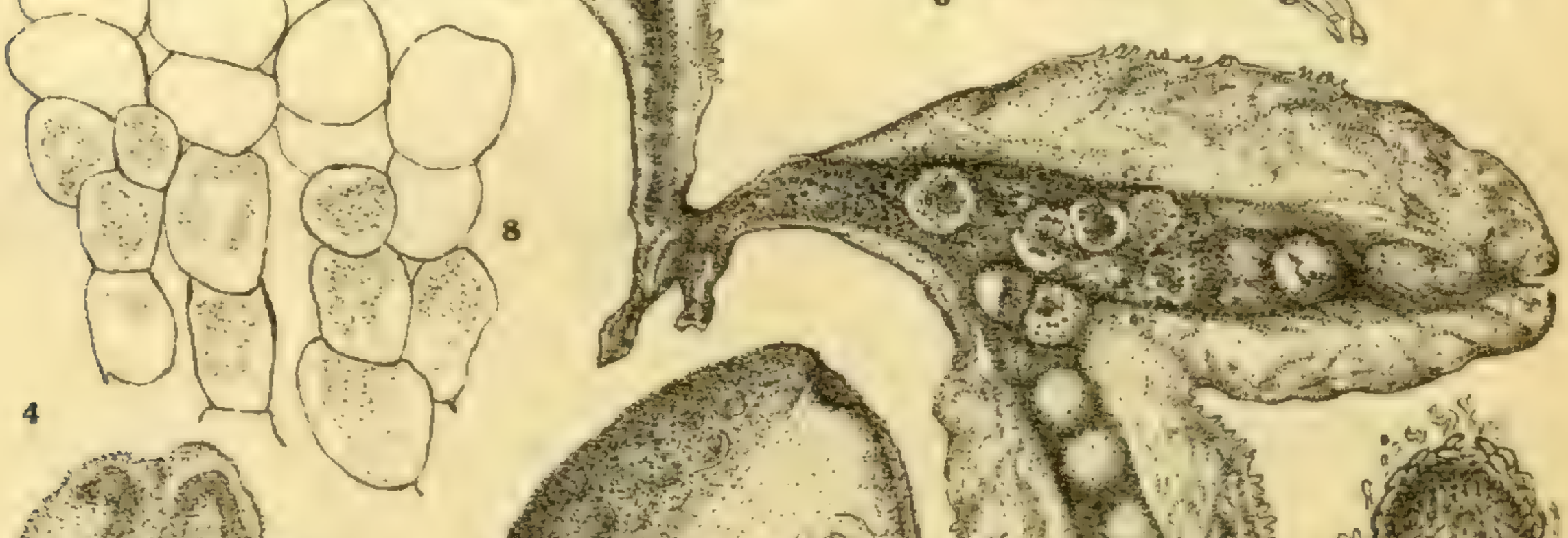

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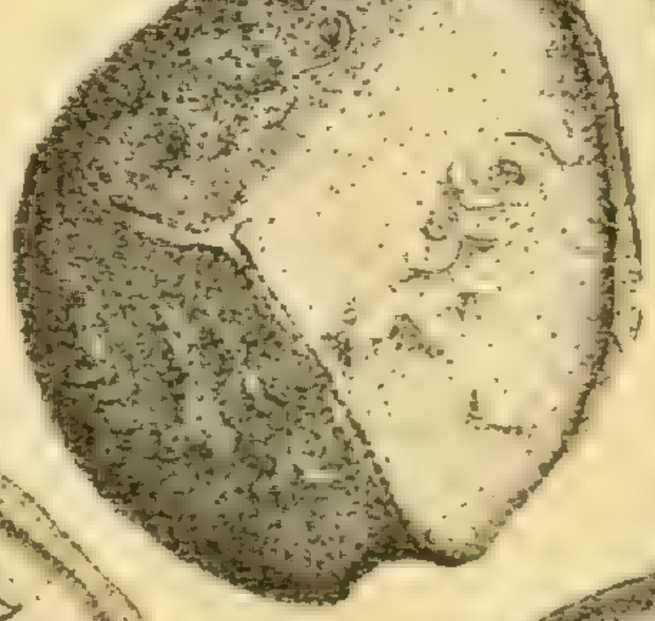
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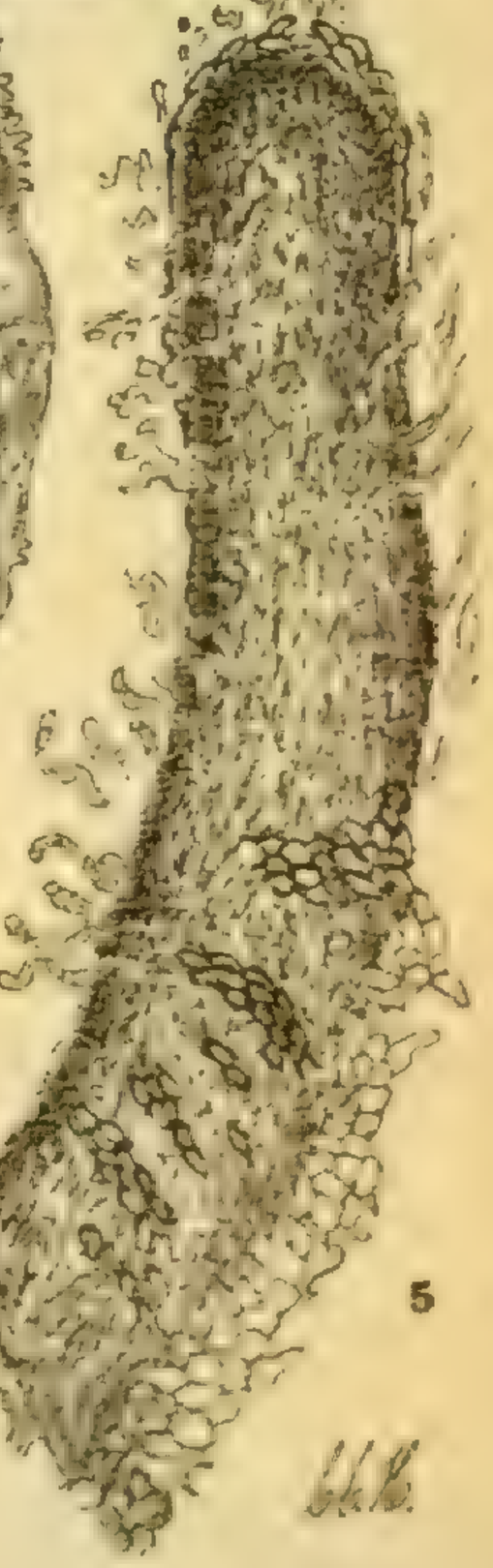

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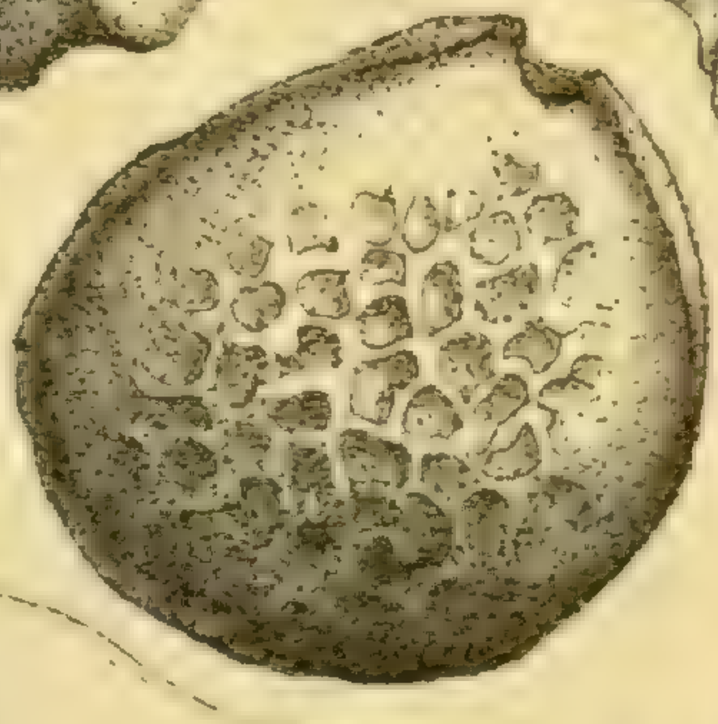

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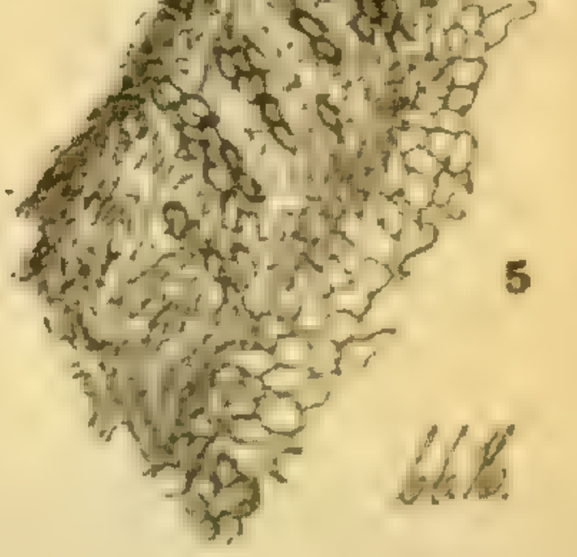
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RICCIA DONNELLII AUST.

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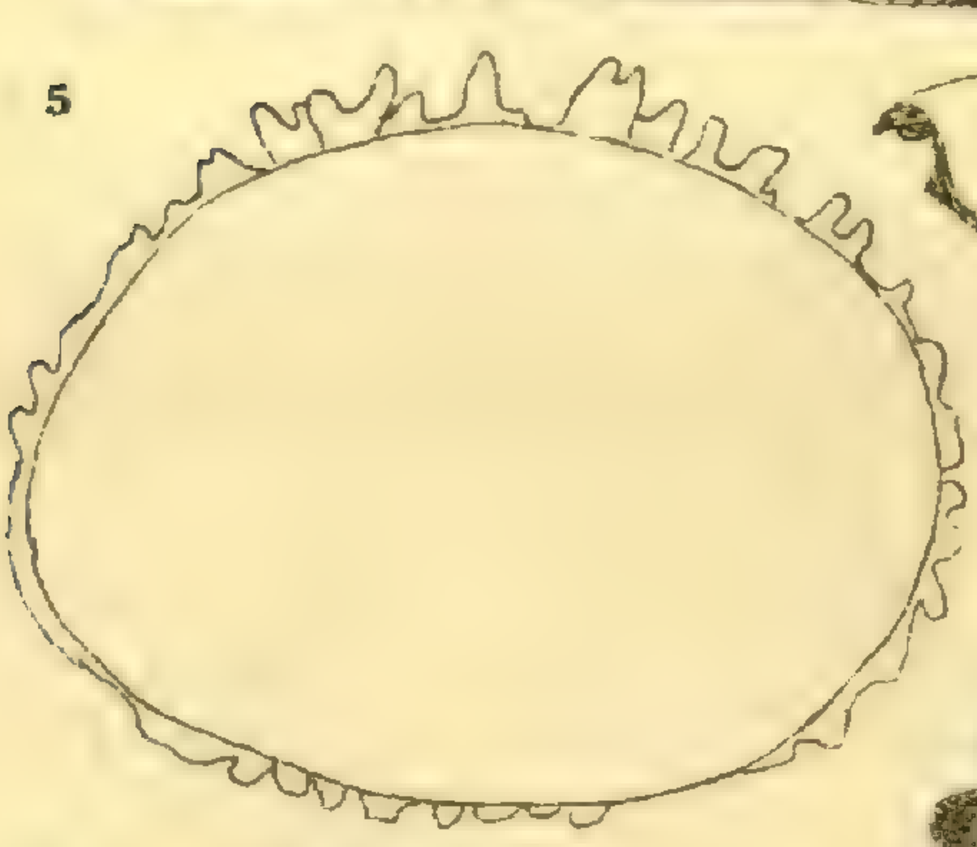

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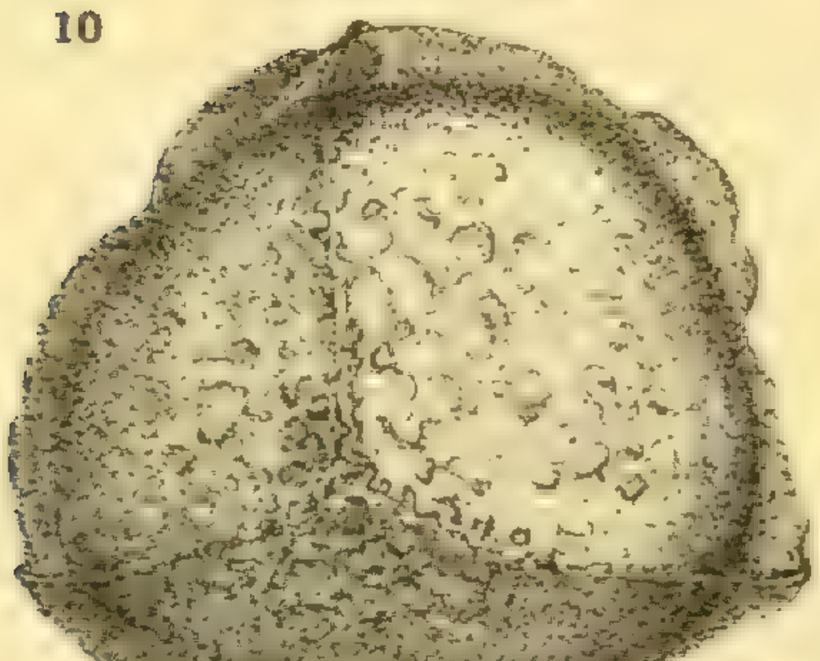

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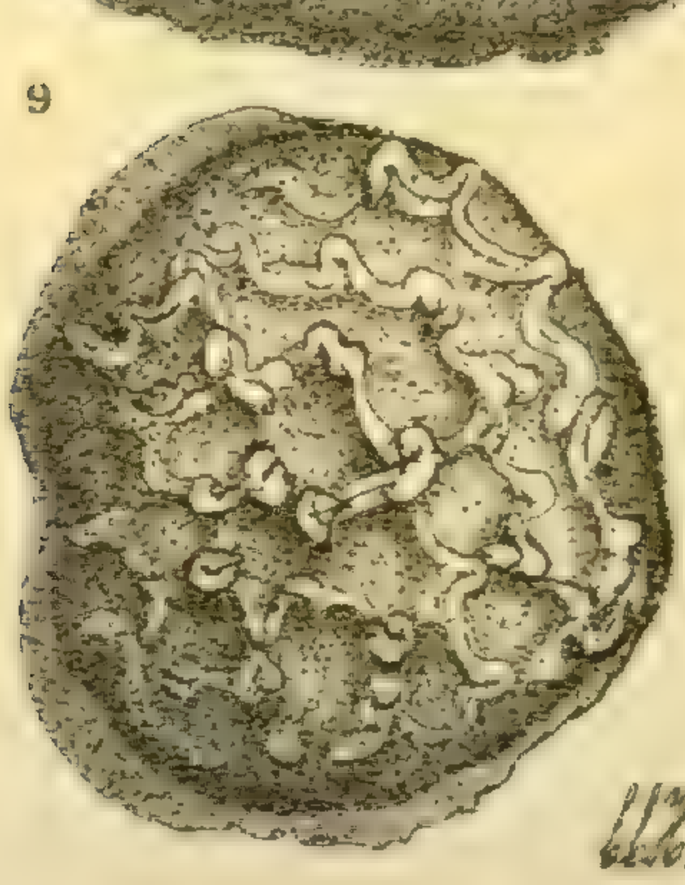

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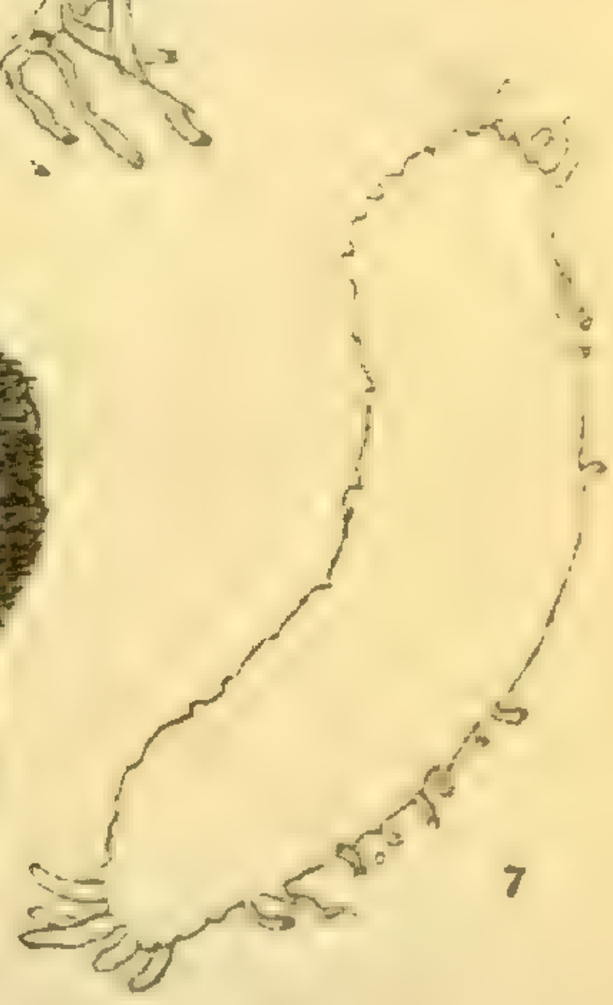

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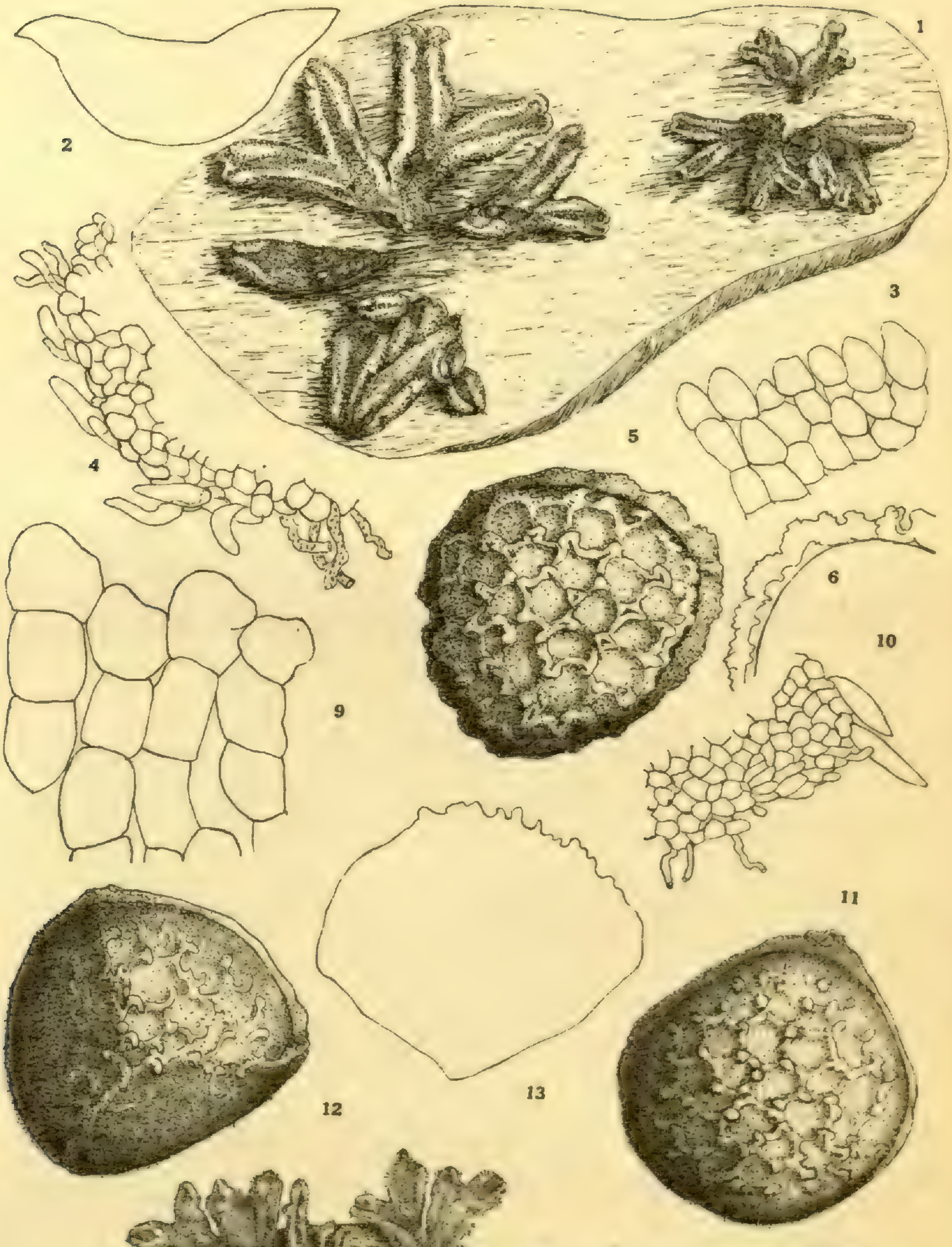
Fig.

1-5. RICCIA DICTYOSPORA M. A. HOWE
6-11. RICCIA BEYRICHIANA HAMPE



1-6. RICCIA ARVENSIS AUST.
7-13 RICCIA HIRTA AUST.

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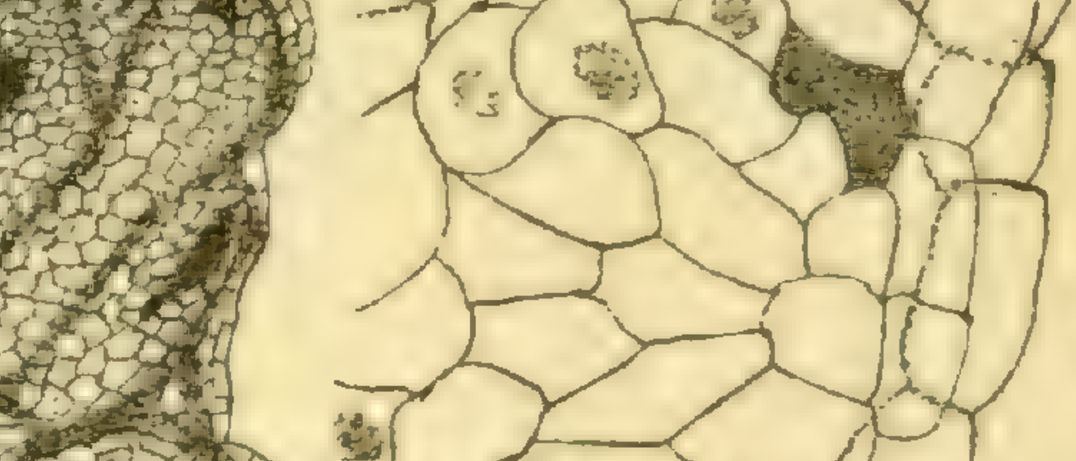
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RICCIA CURTISII JAMES

Vol. 47 No. 8

BULLETIN

OF THE

TORREY BOTANICAL CLUB

AUGUST, 1920

Cell-division of the pollen-mother-cell of Cobaea scandens alba

WANDA KIRKBRIDE FARR

(WITH PLATE 14)

Spindle formation in the pollen-mother-cells of *Cobaea scandens* Cav. was studied by Lawson* in 1898. The stages represented in his plates extend from the resting pollen-mother-cell to the time of nuclear reorganization after the second division. With reference to the division of the cell the following statements are made (pp. 177 and 178):

> There is no cell-plate formed until after the second division. . . . In fig. 24 we see three daughter-nuclei in the same plane. By means of the continuous fibers and mantle-fibers they are connected with one another. These fibers now occupy almost the entire cell-cavity. Cell-plates are now formed in the usual way. Swellings appear on the connecting fibers; these increase in size, and finally result in forming cell-walls which separate the daughter-cells from one another.

A complete disappearance of the spindle-fibers is shown to take place (*f. 21, 22*) before the beginning of the second division. The four nuclei resulting from the second division are arranged tetrahedrally in the mother-cell. Every one of the twenty-four cells figured shows evidence of a thickening of the mother-wall.

The behavior of the cells in *Cobaea*, as reported by Lawson, resembles in some respects that of the pollen-mother-cells of *Nicotiana Tabacum*, *Primula sinensis*, *Tropaeolum majus*, and certain other dicotyledons in which cell-division was found by C. H. Farr† to be accomplished, not by the formation of a cell-plate,

[The BULLETIN for July (47: 279–324, *pl. 10–13*) was issued August 9, 1920]

* Lawson, A. A. Some observations on the development of the karyokinetic spindle in the pollen-mother-cells of *Cobaea scandens* Cav. Proc. California Acad. Sci. Bot. III. 1: 168–188. *pl. 33–36*. 1898.

† Farr, C. H. Cytokinesis of the pollen-mother-cells of certain dicotyledons. Mem. N. Y. Bot. Gard. 6: 253–317. *pl. 27–29*. 1916.

but by a process which "involves the furrowing of the protoplast in the plane midway between the nuclei."

The reports of earlier investigators indicated that the majority of dicotyledons formed their microspores by quadripartition. Concerning the details of the process the literature is somewhat inconsistent, as the following summary indicates:

Juel (1900) in the study of *Syringa;* Tischler (1906) in *Ribes, Bryonia, Mirabilis*, and *Potentilla;* and Duggar (1899) in *Bignonia,* stated definitely that cell-plates were formed, but they furnished no details of the process and no figures to illustrate it.

Baranetsky (1880) in his study of *Lathyrus, Hesperis*, and *Ipomoea*, was unable to find cell-plates. His figures show an incipient furrowing of the protoplasts, but he made no comment upon this fact.

Rosanoff (1865) in *Acacia;* Ishikawa (1911) in *Dahlia;* Osawa (1913) in *Taraxacum;* Miss Pace (1912) in *Parnassia;* Shoemaker (1905) in *Hamamelis;* Miss Fraser (1914) in *Vicia;* and Beer (1912) in *Crepis*, indicated in their drawings the absence of cell-plates during cell-division. These authors do not discuss the possibility of cell-division by any other process.

Pringsheim (1859) in the study of *Dahlia;* Rosenberg (1907) in *Hieracium;* and Guignard (1897) in *Magnolia,* likened these forms, in their method of division, to other forms in which the process involved had not been clearly established.

Miss Digby (1912) in the study of *Primula*, and Cannon (1903) in cotton, discussed and figured the constriction of the pollen-mother-cells but failed to state whether or not cell-plates were formed.

A difference of opinion arose concerning the process of division in the pollen-mother-cells of *Althaea.* Wimmel (1850) reported cell-plates; von Mohl (1853), a combination of cell-plates and furrowing; and Pringsheim (1854) reported furrowing. The assertions again lack the necessary background of detail.

Gates (1907) showed a cell-plate in a diagram of a pollen-mother-cell of *Oenothera.* It is accompanied by no explanation of the process.

Naegeli (1842) in *Oenothera, Bryonia*, and *Cucurbita Pepo;* Sachs (1872) in *Tropaeolum;* Strasburger (1873) in *Tropaeolum;*

Lawson (1898) in *Cobaea;* Tischler (1906) in *Bryonia* and *Ribes;* the same author (1908) in *Podophyllum;* and Johnson* (1914) in *Peperomia,* indicated by their figures a type of division differing from that in which cell-plates are formed. In every instance, however, the statement was made that cell-plates were formed.

Miss Nichols (1908) in her study of *Sarracenia* reported a process of division by constriction of the protoplast, but gave no figures to support the idea.

Andrews (1901) reported a combination of cell-plates and furrowing in the division of the pollen-mother-cells of *Magnolia.* No details of the process were discussed.

The early studies of Wimmel (1850) upon *Althaea* and of Hofmeister (1867) upon *Passiflora* indicate, in the light of the recent study by C. H. Farr, a grasp of the essentials of the furrowing process. Perhaps the lack of detail in their presentations, followed by the launching of the more carefully established cell-plate theory, accounted for the lack of recognition of furrowing as a distinct type of pollen-mother-cell division. Special mention is also due Cannon and Miss Digby, who discussed and figured constriction furrows but failed to report the absence of cell-plates; to say nothing of the large group of investigators whose figures indicate the absence of a cell-plate, but who do not commit themselves concerning the nature of the division.

Such fragmentary and contradictory evidence, however, had resulted in leaving the general impression that quadripartition in dicotyledons was accompanied by the formation of cell-plates. It remained for the presentation of a more complete series of stages from the dividing pollen-mother-cells of *Nicotiana Tabacum,* as presented in C. H. Farr's paper, to clearly establish the process of quadripartition by furrowing. It is there shown that the nuclei of the pollen-mother-cells enlarge during pre-synapsis and synapsis; that a thickening of the mother wall also begins during synapsis and continues throughout the nuclear divisions; and that no cytoplasmic division occurs after the first nuclear division. During the metaphases of the homoeotypic division the remaining

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* Johnson, D. S. Studies of the development of the Piperaceae,—II. The structure and development of *Peperomia hispidula.* Amer. Jour. Bot. 1: 323–339. *pl. 36–38.* 1914. Other references to the papers here cited are given by C. H. Farr.

spindle-fibers of the first division entirely disappear. After the four nuclei resulting from the second division have been fully reorganized, they assume a tetrahedral arrangement in the cell, and a spindle is formed between every two nuclei, making a total of six spindles. "These spindles," as Farr states, "are indistinguishable from each other, in other words it is not possible to tell, either from the nuclei or from the spindles, which of the four nuclei are sister nuclei." A migration of the nuclei occurs resulting in their appression to the plasma-membrane. The cell cavity then becomes lobed. This, it is further shown, appears to be "due to furrowing of the plasma-membrane along the plane midway between each pair of nuclei. The first indication of the furrowing is to be found in the flattening of the protoplast on four sides, each of which is parallel to the plane of three nuclei, so that the entire protoplast assumes the form of a tetrahedron, the nuclei lying near the corners." The furrowing of the plasma-membrane and the invagination of the mother wall take place simultaneously. The furrowing, however, progresses more rapidly at some places than at others. C. H. Farr's description continues as follows:

> It is evident that if there are four nuclei arranged tetrahedrally and equidistant from each other within a sphere, there will be four points upon the surface of that sphere which are equidistant from each of three of the nuclei. . . . By the transformation of the sphere into a tetrahedron the plasma-membrane has been brought closer to the nuclear-membrane. At these four points above mentioned, on the plasma-membrane, the constriction of the mother-cell continues to proceed more rapidly than elsewhere. . . . These projections, or invaginations, continue to elongate toward the center of the cell, and consequently in the direction of the fourth nucleus, keeping at all times equidistant from the three nuclei. As a result the four projections meet in the center of the tetranucleate cell, and fusion of their tips occurs. . . . Thus there are organized four protoplasmic masses each with a single nucleus and connected with each of the other four by an isthmus of cytoplasm, at first quite broad. . . . Apparently each isthmus constricts independently of the others. . . . Upon the completion of the division each of the four cells is separated from the other three by a lateral wall which is thicker in its periphery and thinner at its center.

The figures of *Cobaea scandens*, drawn by Lawson, show the absence of division of the cell after the first nuclear division; the disappearance of the spindle of the first division before the beginning of the second division; the thickening of the cell wall; the tetrahedral arrangement of the four nuclei; and a furrow-like indentation of the plasma-membrane. These characteristics suggest a type of cytokinesis similar to that of *Nicotiana*. The

plant at least presents for study an instance of quadripartition with no conclusive evidence concerning the presence or absence of a cell-plate during the process of division.

MATERIAL AND METHODS

The material for study was collected from plants of *Cobaea scandens alba* growing in the greenhouse of Columbia University. The large size of the pollen-mother-cells made it possible to determine the stages of their development in the fresh mounts. Upon examination it was found that the cells in all of the anthers of the same bud were in approximately the same stage of development. The material for fixation was then selected by examining one anther from the bud and fixing the four remaining anthers of those which were found to be in the desired stages.

Flemming's strong chromic-acetic-osmic fixing solution was used in the preparation of the material. The sections were made 3–5 μ in thickness, and were stained with Flemming's triple stain.

OBSERVATIONS

The mother-cell at the close of the second nuclear division is very nearly spherical in form. The four nuclei are arranged at this stage and through all of the succeeding stages of microspore formation in a tetrahedral manner within the cell. They are ellipsoidal in form. Their diameter immediately after reorganization is about one-seventh of the diameter of the mother-cell, or 6 μ. An enlargement of the nucleus also takes place during the division of the cell, which results in a diameter of about one-fifth of the mother-cell, or 8.4 μ. The chromatin is at first appressed to the nuclear membrane (FIG. 1.). During the later stages of cell-division it is found scattered throughout the nucleus (FIGS. 3, 4, 7). The nuclei contain one or more larger and several smaller nucleoli, which are usually spherical. Occasionally an oval one may be found among the larger nucleoli. In some sections they are seen to be appressed to the nuclear-membrane (FIGS. 1, 2).

The spindles, of which there are six, a spindle connecting every nucleus with every other one, appear to be inflated (FIG. 1). Spindle-fibers may be found to run along apparently the entire distance from one nucleus to another, and they are quite uniform

in thickness throughout their length. Continuous fibers at the extreme outer portion of the spindle may sometimes be found appressed to the plasma-membrane at about their middle points. In the center of the cell the outer fibers of the spindles are seen to cross one another, and leave no inter-spindle areas except a small, usually triangular space at the center of the cell, due to the curvature of the fibers (FIG. 1).

The spindle-fibers in the *Cobaea* exhibit a very different behavior during cell-division than do the spindle-fibers of the larch and onion, as shown by Timberlake.* In the pollen-mother-cells of the larch and in the vegetative cells of the onion, whose divisions are accompanied by the formation of a cell-plate, the continuous fibers, after nuclear division, show a thickening at their ends near the nuclei. This apparently marks the beginning of the activity of the fiber, which soon develops a very marked thickening in the equator. These enlargements upon the fibers seem to unite and form a layer throughout the thickness of the original spindle. This is accompanied by a shortening of the fibers. The central fibers then continue to shorten until they finally disappear, having been used up in the formaton of the cell-plate. While these activities of the fibers are going on, there appears, in the onion, a zone of orange-staining material, presumably carbohydrate in nature, the probable function of which is to serve as reserve material for cell-wall formation.

The continuous fibers in *Cobaea*, in some cases, show a certain amount of thickening throughout about two-thirds of their length, but they remain attenuated at their ends (FIGS. 2, 7). Occasionally a fiber may be found to be thickened apparently throughout its length (FIGS. 5, 7, 8). This thickening, however, is almost negligible when compared with that found in cell-plate formation. In no instances were there found, in any spindle-fibers of the *Cobaea*, such localized enlargements as those shown by Timberlake and others to precede the formation of a cell-plate. No shortening or disappearance of the fibers in any other manner could be found. The continuous fibers between the nuclei are apparently unchanged during the succeeding stages of cell-division (FIGS. 2–7). They

* Timberlake, H. G. The development and function of the cell plate in higher plants. Bot. Gaz. **30**: 73–99, 154–170. *pl. 8, 9.* 1900.

seem to be some of the last structures in the cytoplasm to be severed before the separation of the daughter-cells (FIGS. 6, 7). Even after this separation finally occurs the halves of these fibers are found to extend from the nuclei to the plasma-membranes of the two microspores separated by the furrows. The behavior of the fibers in connection with the formation of the cell-plate led Timberlake to say, "the whole process seems to indicate a somewhat plastic character of the fiber." The behavior of the fibers of *Cobaea*, as shown by the present study, suggests that such a statement would not apply to them, but that they are more permanent in nature.

Across the equators of the spindles a less dense region of cytoplasm appears at about the time of thickening of the fibers (FIG. 2). This also is evident during the remaining stages of division (FIGS. 3–7). It is apparently made more conspicuous by a denser area around the nuclei, which does not extend into the equatorial regions. The peripheral cytoplasm is fibrillar in nature. The fibrillae show at first no tendency to radiate from the nuclei (FIG. 1). The beginning of such a radiation can be seen in FIG. 2. This continues until a distinct radiation is found in the stage represented by FIG. 4, and the condition is maintained throughout the succeeding stages of division. Scattered irregularly through the cytoplasm are many spherical, red-stained bodies which vary greatly in size. In FIG. 3 five such bodies are shown, which appear to be arranged along a fiber, but in general they have no definite arrangement with reference to any other structures in the cell.

Very soon after the completion of the second nuclear division the cell-wall becomes thickened to about one-fifteenth of the diameter of the mother-cell. This thickening is approximately uniform over the entire surface of most of the cells examined. The loose arrangement of the cells in the pollen-chamber may account for this uniform enlargement. The intercellular spaces are usually large enough to prevent the touching of the different cells. Occasionally they may be found in groups of two or three with the walls of the different cells appressed. At this early stage in division the cell-wall has reached almost its maximum thickness. Cells were rarely found whose wall-thickness exceeded one-fourteenth to one-thirteenth of the diameter of the mother-cell.

After the completion of the second nuclear division, the most striking change in the pollen-mother-cell is its lobed appearance. Upon the plasma-membrane, midway between the polar regions of the three nuclei, there appear sharp indentations pointing toward the center of the cell. In a section, three of these may be in view. FIG. 2 clearly shows two such indentations. The absence of the third one is due to the plane in which the section is cut. The view of the adjoining spindle shows that it is not a median section, such as we have in the two other spindles. The cell-wall conforms to these indentations and the fibers through which the furrows pass, aside from being separated in the center, are apparently undisturbed by it.

During the succeeding stages of division there appear in some of the sections, first at the periphery of the spindle equators, later at different points in the equators, small masses of material which vary in their staining reactions according to their size. The smaller ones stain very darkly, almost black, with gentian violet (FIG. 3). The larger ones stain the same as the cell-wall, with a narrow, dark-stained layer of material upon the outside, apparently a membrane (FIG. 7). These bodies do not appear in all of the sections, but they occur in short rows directly in front of the furrow tips, as shown before one furrow in FIG. 5. They are not seen at this time either along the centers of the spindles or in the center of the cell. If any such bodies were present, beyond these short rows, they would be clearly visible because of the regions of less dense cytoplasm across the equators of the spindles.

A careful examination of the sections in which these masses of material appear has resulted in the conclusion that they are never upon the spindle-fibers, but that they are between them; and that the spindle-fibers have no direct relation to their formation. They are believed to be sections of the furrows which are cutting into the cytoplasm of the pollen-mother-cell. In a section such as that shown in FIG. 3, for instance, there has been cut a portion from one of the faces of the tetrahedral mother-cell, and in it are median sections of three nuclei. If in the unsectioned mother-cell every one of the spindles is cut by a furrow, it can be seen that in cutting off this portion from the mother-cell, three half-furrows have been removed. If this severed portion is viewed upon the

side opposite to the cut surface, there are seen the three lobes of the mother-cell and the three half-furrows meeting at a point equidistant from the centers of the three lobes. These furrows are cutting sharply into the cytoplasm. It has been stated before that the equatorial regions through which these furrows are advancing are composed of very clear cytoplasm. There are then no visible structures in the line of advance of the furrows except the spindle-fibers. An examination of the cut surface of the section will show that the furrows work in between the fibers in their paths, and later surround them. A cross-section of such a furrow would present a wavy appearance upon its advancing edge. The masses of material which appear in the equatorial regions, as shown in FIGS. 3, 5 and 7, are the severed portions of this edge. The smaller portions consist of the plasma-membrane, while the larger portions are of wall material surrounded by plasma-membrane. It may also be observed that these penetrating tips appear first at the peripheral regions of the equators of the spindles. This is what might be expected if the furrow advances uniformly throughout its length.

C. H. Farr found in *Nicotiana* that the furrows advance much more rapidly than elsewhere from the points of intersection of the six furrows. As he states,

> It is thus apparent that these four projections finally meet in the center of the tetranucleate cell, before the furrows have completed the division on the equator of each spindle. . . . . The first indication of the growth of thes eprojections toward the center of the cell is in the straightening of the spindle-fibers. . . . . This straightening results in the fibers pulling away from the center of the mother-cell, leaving a space which is triangular in section, but is really pyramidal, in the center of the cell.

The projections in his plant are also triangular in section and, in his *f. 32*, are shown as they appear during the earlier stages of furrowing.

In the corresponding stages of *Cobaea* no traces of such projections from the intersections of the furrows could be found (FIGS. 3, 4, 5). While in the tobacco the furrows are found to penetrate more deeply at four points, the furrows of *Cobaea* may be conceived of as advancing, in general, more regularly, penetrating only slightly deeper at many points upon their edges. That the appearance of these furrow tips in the sections is due to the planes in which they are cut may be seen from a comparison

of FIGS. 4 and 5. These are adjoining sections of the same pollen-mother-cell. FIG. 4 is drawn from a section cut between FIG. 5 and the fourth nucleus of the cell. Fig. 4 is consequently nearer to the furrows which are advancing from the sides of the lobes, nearer to the fourth nucleus. The projections are very distinct in FIG. 4, but they have not advanced far enough into the cytoplasm to be seen in the section from which FIG. 5 is drawn.

In the center of the cell section, FIG. 6, at the point toward which the tips of the three furrows are pointing, is shown the first appearance of that which will develop, at an even later stage, into the central triangular area of wall material. No straightening of the fibers may be observed to precede it. FIG. 7 represents a very late stage in the process of cell-division, in which the central triangular area may be seen. The furrows have pushed through in other places along the equators of the spindles. Some of the fibers in their paths are not yet surrounded, as can be seen from the drawing. These observations show that except for these slight irregularities the advance of the furrows in *Cobaea* is quite uniform, as has been suggested in connection with their appearance first at the outer portions of the spindle equators. This uniform advance accounts for the appearance of the central triangular section of the furrow at a much later stage than it was found to appear in *Nicotiana*. The daughter cells become almost spherical in form before their complete separation (FIG. 7).

DISCUSSION

The pollen-mother-cells of *Cobaea*, then, present another instance in the microspore formation of dicotyledons, in which the cell-plate is not apparent during cytoplasmic division. The process concerned is, in its general characteristics, like that found by C. H. Farr in *Nicotiana* and other dicotyledons. It differs from *Nicotiana*, however, in possessing some cytoplasmic characteristics similar to those observed in the study of cleavage furrows in the fungi. Mention has already been made of the less dense areas in *Cobaea* which appear across the equators of the spindles during the process of furrowing. Now Harper* found

* Harper, R. A. Cell and nuclear division in *Fuligo varians*. Bot. Gaz. **30**: 217–251. *pl. 14*. 1900.

in the study of spore formation in *Pilobolus* and *Fuligo* that a differentiation of the cytoplasm might occur during the process of cleavage. He found "hyaline areas" occurring midway between each pair of nuclei. According to his account the cytoplasm appears as if the protoplasmic mass had contracted about each nucleus as a center, thus leaving irregular, furrow-shaped, less dense spaces in the middle region between the two nuclei.

In *Cobaea* the less dense areas referred to above are practically free from any granular masses, and appear very clear. The term "hyaline areas" has not been used because the discussion and figures by Harper concerning the somewhat similar regions in the dividing cells of the fungi indicate a condition of greater transparency than is evident in *Cobaea*. These areas also do not appear so markedly wedge-shaped as those shown by Harper in *Fuligo* (*f. 8*). They are, however, in general form, not at all unlike that shown by the same author in his *f. 9*. Aside from these differences, the description of the "hyaline areas" in *Fuligo* and *Pilobolus* might be applied directly to the less dense areas in *Cobaea* without any alteration.

The appearance of such cytoplasmic differentiation in these widely separated forms would seem to be of significance in establishing the similarity of the processes concerned in the divisions by furrowing, and would also give strength to the idea that they are worthy of all of the recognition given them by Harper in the fungi. Since these less dense areas may be found to occur in both dicotyledons and fungi, it must be remembered that the conditions under which they are found are quite similar. In all cases they appear in connection with the cytoplasmic division of a multinucleate cell in which cell-plates are not formed. In all instances so far reported they bound off a single nucleus and never a group of nuclei. They are also the early indicators that the process of cleavage will result in uninucleate masses with approximately equal amounts of cytoplasm.

A comparison of the pollen-mother-cells of the two forms with reference to the breadth of the progressing furrow will show that they are much more narrow in *Cobaea* than in *Nicotiana*. A further comparison of the maximum thickening of the cell-walls in the two forms shows that it reaches a thickness of one-tenth of

the pollen-mother-cell in *Nicotiana*, while in *Cobaea* it thickens to only one fifteenth of the mother-cell diameter.

If the cell-wall material is colloidal in nature, the degree of its plasticity would be related to the amount of swelling due to imbibition. This suggests a possible relation between the amount of thickening in the wall and the breadth of the furrow. If in a pollen-mother-cell such as that of *Nicotiana* there is an almost negligible degree of resistance of the cell-wall to the forms assumed by the protoplast, as suggested by C. H. Farr, the pollen-mother-cell-wall of *Cobaea*, which thickens less, might be conceived of as producing a greater resistance to the cell within. The relative surface tension of the protoplast, together with the less plastic cell-wall, might prevent the early rounding up of the lobes of the mother-cell of *Cobaea*, and thus decrease the breadth of the furrow.

The conditions reported in the microspore formation of *Drosera*, by Levine,* suggest a further application of this idea. In that case no cell-plates could be determined during the division of the cells, and they did not present the marked characteristics of a process of division by furrowing. Levine states: "if furrows are present in *Drosera* they must be extremely narrow like those shown in the slime moulds by Harper ('00, '14), which proceed from the periphery to the center of the cytoplasm." The cell-wall of the pollen-mother-cell of *Drosera* thickens to only one-twenty-second of the diameter of the protoplast, and if the previous suggestions are assumed, would exert an even greater degree of resistance to the protoplast than that of *Cobaea*. This may perhaps be great enough to account for an extremely narrow furrow. The fact that the pollen-mother-cells do not separate after cell-division is completed, but form a tetrahedral pollen-grain, may also be of significance in this relation.

It has been observed that some forms of amoeba before making contact with a food particle send forth strands of protoplasm, or pseudopodia, and surround the food. A fusion of these pseudopodia at their free ends or edges results in the complete enclosure of the food. In *Cobaea*, as has been previously stated, the advancing tips of the furrows are seen first between the spindle-

* Levine, M. Somatic and reduction divisions in certain species of *Drosera*. N. Y. Bot. Gar. Mem. **6**: 127–147. *pl. 16–19*. 1916.

fibers, and later they appear to surround them. These observations, together with the appearance of the spindle-fibers throughout cell-division and after division is completed, lead to the conclusion that the fibers are first surrounded and then severed. In considering such a progressing furrow with relation to the fibers, the behavior of the amoebae toward their food particles suggests itself as an analogy. The apparently very elastic plasma-membrane plays a prominent part in both instances. In the process of furrowing the spindle-fiber corresponds to the food particle. It does not seem entirely inconceivable that the advancing edge of the furrow, amoeba-like, may approach a fiber to within a certain distance and then send forth projections which first surround it and finally cause it to separate at its middle point.

The cleavage in *Cobaea*, as has been shown, is directed with reference to the distribution of the nuclei. It seems quite possible, as was suggested by Harper for *Fuligo* and *Pilobolus*, that the nuclei may control the orientation of the furrows, and that the formation of the less dense zones in the cytoplasm is a visible expression of the activity of the nuclei. If to these assumptions are added the suggestions of C. H. Farr, concerning the diffusion of soluble ions from the nuclei along the paths of the fibers, a possible explanation for an amoeboid activity suggests itself. If the fibers mark the paths of diffusion, the compounds formed by the meeting ions would be most concentrated around the fibers in the exact equatorial planes. It does not then seem unthinkable that in these regions of highest concentration the substances may be in the necessary condition to contribute to the development of the plasma-membrane, and that in this manner they determine the position and direction of the penetrating furrows.

To Dr. R. A. Harper I wish to express my appreciation for advice and inspiration during the progress of this study.

DEPARTMENT OF BOTANY,
COLUMBIA UNIVERSITY

Explanation of plate 14

The figures were drawn with a Spencer 1.8 objective and ocular 4, with a tube length of 170 mm. The magnification is about 1,971 diameters.

FIG. 1. Mother-cell after second nuclear division. Nuclei are organized, spindles inflated, and wall thickened.

FIG. 2. An early stage in the furrowing process, showing thickened fibers and the first appearance of less dense areas.

FIG. 3. Furrows penetrating deeper, fibers undisturbed in position, and tips of furrows between fibers.

FIG. 4. A section with deeper furrows, showing no penetrating tips in the less dense areas.

FIG. 5. Another section from the cell represented in FIG. 4, between that section and the fourth nucleus, showing penetrating tips of furrows between the fibers.

FIG. 6. Narrow continuous furrows, tips of furrows, and the beginning of a central triangular area.

FIG. 7. Late stage in division, showing continuous fibers, surrounded fibers, central triangular area, and the rounding up of the daughter-cells.

Apogamy in Osmunda cinnamomea and O. Claytoniana

ELIZABETH DOROTHY WUIST BROWN

(WITH 10 TEXT FIGURES)

The occurrence of apogamy in *Osmunda cinnamomea* L. and *O. Claytoniana* L. is of especial interest, since the only reported case of apogamy in this genus is given by Leitgeb.† He does not state definitely in which species he observed apogamy but presumably it was in *O. regalis* L. His observations have never been confirmed, although attempts have been made by workers to induce apogamy in this fern under varied cultural conditions.

The cases of apogamy described in this paper occurred in cultures of *Osmunda cinnamomea* and *O. Claytoniana* with which, together with *O. regalis*, experiments were made during the years 1916–18 in the Osborn Botanical Laboratory of Yale University. The writer is especially indebted to Professor A. W. Evans for many helpful suggestions and criticisms.

MATERIAL

The spores of *O. regalis*, *O. cinnamomea* and *O. Claytoniana* were collected from two sources: from sporophytes growing on lawns about New Haven, Connecticut, and from sporophytes growing under natural environmental conditions in Beaver Swamp, a short distance from that city. No differences were observed in the growth and development of the prothallia from the two sources.

Collections of fertile fronds were made in late June and cultures were made early in July. The cultures were made by sowing the spores on 26 c.c. of Prantl's and Knop's nutrient solutions and their modifications, to which had been added a drop of a 1 per cent solution of ferric chloride, in small glass capsules.

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* Contribution from the Osborn Botanical Laboratory.

† Die Sprossbildung an apogamen Farnprothallien. Ber. Deutsch. Bot. Ges. **3**: 169–176. 1885.

The formulas for these solutions are as follows:

I. PRANTL'S SOLUTION (PRANTL '81)

K_2SO_4.....0.70g.
NaCl.....0.23g.
$CaSO_4$.....0.70g.
$MgSO_4$.....0.50g.
Na_3PO_4.....0.50g.
NH_4NO_3 solution, 0.064 per cent..20 c.c.

II. KNOP'S SOLUTION

$MgSO_4$.....0.25g.
$Ca(No_3)_2$.....1.00g.
K_2HPO_4.....0.25g.
KCE.....0.12g.

In the following modified solutions the items not mentioned are the same as in the corresponding unmodified solution:

I. PRANTL'S SOLUTION

I *a*. NH_4NO_3 omitted
I *b*. K_2SO_4 omitted
I *c*. NaCl omitted
I *d*. $CaSO_4$ omitted
I *e*. $MgSO_4$ omitted
I *g*. NaCl and Na_3PO_4 omitted

II. KNOP'S SOLUTION

II *a*. $Ca(NO_3)_2$ omitted

After the spores had been sown the cultures were placed before an east window and the culture solutions were not renewed. It was only during the period of germination that the cultures were exposed to the direct rays of the sun for a short time each day. If left longer the solution became heated and the prothallia died.

DEVELOPMENT OF PROTHALLIA AND SEX ORGANS

Germination, in all three species, began in a few days after the spores were sown.

O. regalis.—Three weeks later the prothallia of this species varied in the different cultures from four to fifty-nine cells, the greatest irregularity in size occurring in cultures of I*c*. On the whole greater growth occurred in cultures of the modified than in those of the unmodified solutions, and this was especially true in the case of I*a*. Here the amount of nitrate present was evidently sufficient to meet the needs for the growth of the prothallia and the effect of the unbalanced solution tended at first to stimulate rather than retard the growth. However, the reverse was true in the later development of the prothallia, for at the end of the fourth month in I*b*, I*c*, I*d*, I*g*, and II*a* the majority of the prothallia were dead; in I*a*, I*f*, and I*g*, although the prothallia were alive, growth was much slower.

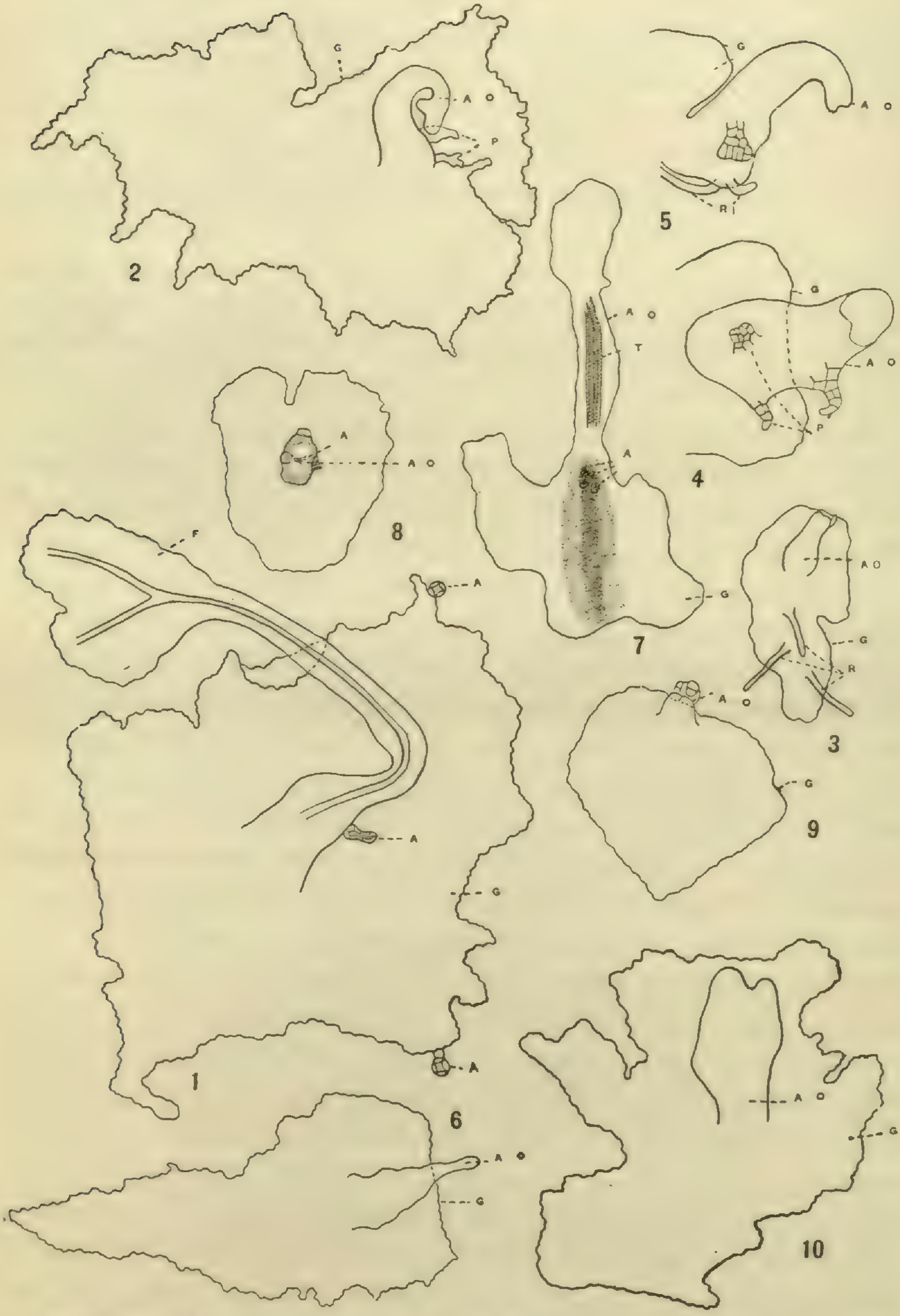
Campbell* states, "in . . . *O. regalis* it is quite common to

* Mosses and Ferns, p. 340. London. 1895.

have the first transverse wall followed by a longitudinal wall in each cell, so that the four primary cells are arranged quadrantwise." While in general this was the order of development, yet in some of the cultures a filamentous stage of two and three cells was formed before longitudinal division took place. Even in those cases where the four primary cells were arranged quadrantwise the prothallia tended to assume an elongated form and not a cell mass at first. In I*d* the prothallia were very broad and frequent branching occurred at the expanded apices of the prothallia. In I*e* and I*f* the growth was very irregular, some of the prothallia tending to assume an elongated form and others a broad form. Branching in these cultures was rare; in I and II*a*, however, it was common, the branches often occurring as filamentous outgrowths at the bases of the young prothallia, which were decidedly filamentous in form. In some cases this was so marked that a reversion of the prothallia at its apex to a filamentous condition took place. Large heart-shaped prothallia, monoecious in most cases, were present in the unmodified solutions. No cases of apogamy in the species were observed.

O. cinnamomea.—Growth in this species during the first three weeks was not so rapid as in *O. regalis*, for the largest prothallia were only thirty-four cells in size and the smallest two cells. As in *O. regalis* greatest growth took place in I*a*, while least growth occurred in I*b* and I*f*. The early divisions of the prothallia were in keeping with the previously quoted statement of Campbell. However, in many cases in I*a* the filamentous stage consisted of from three to five cells. The young prothallia in most of the cultures were broad in form, sometimes a mere cell mass. In the case of the prothallia in II (Knop's unmodified solution), while the initial divisions were the same, there was more of a tendency for the young prothallia to become elongated and in rare cases a filamentous stage, as many as seven cells in length, was formed before longitudinal divisions took place.

A greater irregularity in the form of the young prothallia occurred in the cultures of the various modified solutions than in the same cultures of *O. regalis*. In I*a*, I*c*, I*d*, I*f* and I*g* the form of the young prothallia was very irregular, this being especially pronounced in I*a* and I*c*. Greater regularity of form occurred



FIGS. 1–7. Apogamous outgrowths of *Osmunda cinnamomea*. FIGS. 8–10. Apogamous outgrowths of *Osmunda Claytoniana*. *AO*, apogamous outgrowths; *a*, archegonia; *a′*, antheridia; *f*, leaf; *g*, gametophyte; *r*, rhizoid, *t*, tracheids.

in I*b* and I*e*. In II*a* the regularity of form was very striking. However, at the end of eight months the greatest irregularity of form was shown by the prothallia of I*a* and I*c*. Many of these were elongated plates of cells with the margins of the apices extremely irregular. Branching of the prothallia occurred in the cultures of the following solutions: I*a*, I*b*, I*c*, I*d*, I*e* and I*g*, being especially marked in I*a*, I*b*, I*c* and I*d*.

Sexual organs, both male and female, developed in various cultures. That some of these were normal was shown by the presence of young sporophytes, which developed only in the unmodified solutions after the nutrient solution had been renewed.

Apogamous outgrowths, developed on prothallia in cultures of the following solutions, eight months and one week (March 9, 1917) after the spores were sown (FIGS. 1–6): I, I*a*, I*b* and I*e*. In another attempt to induce apogamy, prothallia were transferred from cultures of I (Prantl's unmodified solution) to I*a* four weeks after the spores were sown. One case of apogamy in these cultures was observed (FIG. 7).

O. Claytoniana.—At the end of three weeks the average size of the prothallia of this species in the different cultures varied from one to thirty-three cells. As in *O. regalis* and *O. cinnamomea* the greatest growth occurred in I*a*; least growth occurred in I*c*. No filamentous stage was present in many of the prothallia of the unmodified solutions, a longitudinal wall having been formed in the first cell. In other prothallia the filamentous stage varied from five cells in I*c* and I*f* to six cells in II*a*, seven cells in I*c* and II*a* and eight cells in I*c*.

The young prothallia in the cultures of the unmodified solutions I and II and the modified solutions I*a*, I*b*, I*c*, I*g* and II*a* were regular in form, being somewhat elongated. But in I*d*, I*e*, I*f* and II*a* the form of the majority of the prothallia was very irregular; in some cases they were broad, in others elongated. The older prothallia (March 19, 1917) in the cultures of I*a*, I*b*, I*d*, I*g* and II*a* showed the greatest irregularity of size and form. Those of I*d* and I*g* were the smallest in size, while those of I*a* and I*b* were the most irregular in form, some of the prothallia of I*a* being irregular plates of cells.

No branching of the prothallia was observed in the cultures

of I*b* and II while in I, I*a*, I*c*, I*d*, I*e* and I*f* it was rare. In the cultures of I*g* branching of the prothallia was very common. In all cases observed the branching of the prothallia occurred in the younger stages of the development.

Sexual organs were found in the unmodified solutions, while in the modified solutions they were formed only on the prothallia in I*a* and I*b*. However, in the latter only a few sexual organs were observed. Normal sporophytes developed in some cultures of the unmodified solutions after the nutrient solutions had been renewed, and three apogamous outgrowths occurred on prothallia in I*b* (FIGS. 8–10).

DESCRIPTIONS OF THE APOGAMOUS OUTGROWTHS

The apogamous outgrowths in *O. cinnamomea*, as previously stated, developed on prothallia in cultures of I, I*a*, I*b* and I*e*. One developed also on a prothallium which had been transferred from I (Prantl's solution), four weeks after the spores were sown, to I*a*.

The prothallium in a culture of I (FIG. 1), upon which the apogamous outgrowth occurred, was irregular in shape and no sinus was present. Two antheridia developed from marginal cells, one in the expanded apex and one near the base of the prothallium. One of the antheridia was stalked and the other sessile. The prothallium was one cell thick, except for a small region in the center where the meristem is usually formed. In this region a swelling occurred which continued to grow, forming a cylindrical process several cells in thickness. Gradually it assumed the shape of a young leaf and finally developed into a normally appearing leaf consisting of a petiole and a blade bearing a forking rib. On one side of the petiole near its enlarged base an archegonium which appeared normal developed.

The apogamous outgrowth which occurred in a culture of I*a* developed in the same manner as the one just described. This prothallium, also, was approximately the same size and shape (FIG. 2); however, no antheridia or archegonia were formed.

The apogamous outgrowth found in a culture of I*b* developed on a prothallium which was small, elongated and regular in shape. No sinus was present and from the meristematic region near the apex of the prothallium the apogamous outgrowth was formed. It began as a swelling which developed into a cellular mass.

Swollen at its base it narrowed and then enlarged into an apex which was slightly lobed (FIG. 3). This structre continued to elongate and formed a flat, cellular mass which was lobed (FIGS. 4, 5). From near its base and on one side of the structure proliferations of a thallus-like character developed.

The prothallium in the culture of I*e*, which gave rise to the apogamous outgrowth, was wedge-shaped with an obtuse apex without a sinus (FIG. 6). As in the previous cases described the apogamous outgrowth developed as a swelling from the meristematic region. This swelling continued to grow, forming a cylindrical process several cells in thickness which became somewhat narrower as it developed.

An apogamous outgrowth formed on a prothallium which had been transferred from I to I*a*, four weeks after the spores were sown. This prothallium (FIG. 7) was broad and irregular, one lobe being much larger than the other. A meristem was present from which archegonia, normal in appearance, developed. From the margin of the prothallium, where the sinus is usually formed, the prothallium continued to grow into a cylindrical cellular structure, which finally broadened into a flat thallus-like body one cell in thickness with a rounded apex. Tracheids were formed in the narrow thickened portion.

All three cases of apogamy in *O. Claytoniana* were observed in cultures of I*b*, where they developed as cellular masses on the prothallia (FIGS. 8–10). One of these cellular masses, formed as a swelling from the meristem near the center of a heart-shaped prothallium which was distinctly notched, bore on the side near its apex an archegonium (FIG. 8). Another of these cellular masses (FIG. 9) was formed a little to one side of the center of the meristem and near the expanded apex of a prothallium. This outgrowth began as a swelling of the tissue, which was triangular without a sinus, and developed into a mass whose apex was slightly lobed. From one side a proliferation of a thallus-like character developed. The third cellular mass was formed on a very irregular prothallium (FIG. 10). Although the margin was greatly indented in places no apica sinus was present. The apogamous outgrowth, as in the other two cases, appeared first as a swelling of the meristem and then developed into an irregular, cylindrical cellular mass whose apex was distinctly bilobed.

Regeneration in Sphaerocarpos Donnellii

H. W. Rickett

(WITH TWENTY-FIVE TEXT FIGURES)

Regeneration, or the production of adventitious shoots from the vegetative tissue, has been described in *Sphaerocarpos* by Leitgeb (4), C. and R. Douin (2), and Goebel (3). Leitgeb describes regeneration in *S. Michelii* Bell. (*S. terrestris* Sm.) as occurring from both the lobes and the midrib of the thallus. It results from the growth of a single cell into a cylindrical body, whose tip gradually broadens out and becomes flat, forming the normal plant body. As in the case of sporelings, sex organs are formed very early—in some cases before the young shoot has assumed the flat shape.

The Douins (2), studying *S. Michelii* and *S. texanus* Aust. (*S. californicus* Aust.), observed regeneration taking place from the midrib and from the involucres, and state that it probably occurs also from the lobes, though this was not seen by them. Regeneration is most marked in connection with the female thalli. When these are destroyed by drought, the midrib remains alive for some time, and if a period of humidity follows, each fork of the midrib elongates, forming more or less numerous lobes and involucres. Regeneration also occurs from the involucres, when these are accidentally bent over and brought into contact with the soil. Certain cells of the involucre in these cases multiply and give rise to new thalli. The Douins' figures show such plants arising from around the opening of the involucre, in exactly the same way as is illustrated in my Fig. 18. The regenerated thalli are somewhat different from the old ones, especially in the case of the male, showing dorsal lobes, whose form leads the authors to conclude that they are modified involucres.

Goebel (3), working with *S. Michelii* (possibly mixed with *S. texanus*, if the latter species is found throughout Europe as it is in France), found that regeneration occurs when portions of the

thallus, especially the involucres, are broken off or partly broken off, and are in contact with the soil. Regeneration is most easily observed if separated portions of the involucres are cultivated in water. Shoots may be produced either on the inside or on the outside of the involucre, and rhizoids are produced at the same time, especially in the neighborhood of the shoots. When shoots develop on the inside of the involucre, it is necessary for them to curve about so as to emerge; if formed on the outside of the involucre, they grow straight outward. A shoot is formed as a cell mass arising from a single cell. At the tip of this body is formed the growing point. Right and left from this, flat wings develop. Sometimes a long germ-tube is first formed, consisting of many cells. In such a case, the whole structure resembles a sporeling, except that the formation of the flat plate at the end of the germ-tube is not at right angles to the germ-tube, but simply a spreading out and flattening of the latter. The history, except in a few cases, is not so simple as that described by Leitgeb, the wings not necessarily lying in one plane, and the formation of the flat plate resulting from the spreading out of the first cylindrical body. Sometimes one of the wings goes on to develop into a thallus, apparently because the development of the growing region between the two wings was arrested. Goebel compares the formation of these adventitious shoots with spore germination, and emphasizes the fact that they may develop either almost exactly as does a sporeling, namely by the formation of a flat plate of cells from the terminal group of cells of the germ-tube, or by a direct and simple flattening out of the primary cell mass, which fact shows of how little value is any sharp distinction between these two methods in a discussion of spore germination.

I first noticed the occurrence of regeneration in searching for germinating spores in soil cultures of *S. Donnellii* Aust. Many small plants which I picked up proved to have no spore wall attached at the basal end, and in some cases were found instead to be attached to old dead portions of tissue. In these cases the plants were of a ribbon-like form, broadening out a little at the anterior end. In cultures made later for the purpose of obtaining regeneration, the young plants were broader and less ribbon-shaped. The light conditions under which these latter plants

had developed were more favorable. In the cases first noted the young plants were growing among older plants, which overshadowed them to a large extent, and the elongated ribbon form is probably a resultant of these conditions.

Regeneration also occurred from the involucres of several female plants which were being cultivated singly on soil. Conditions here were such as to produce the extreme leafy form of the thallus described in a previous paper (5); as the posterior part of the thallus died, small masses of cells protruded from the involucres in this region and later grew out into young thalli.

Attempts were made to induce regeneration by artificial means, such as the wounding of the female thalli. In cases in which involucres or lobes were almost or completely separated from the plant body, regeneration occurred abundantly, though not usually at points showing any definite relation to the cut surfaces. The rest of the plant continued to grow in a normal manner, although occasionally adventitious shoots were formed on the midrib, often near places where portions had been cut off. I have never observed regenerated shoots to arise directly from one of the wounded surfaces. Very frequently rhizoids developed from the cut end of the separated portion of the thallus; these appeared without any spatial relation to the adventitious shoots and sometimes before the latter became evident.

Attempts were also made, in every case unsuccessfully, to induce regeneration, using the same or similar methods, from the sex organs, and also from young sporophytes.

The occurrence of regeneration is frequent in cultures, especially from the female thalli, and seems to be a regular method of vegetative multiplication, rather than merely a response to abnormal conditions. After the development of sporophytes, the mother plants often die in large part, and growth continues after a time by means of regeneration from their surviving portions. C. Douin (1), describing the life history of *S. Michelii* under natural conditions in Europe, states that the old thalli are usually buried by the tilling, and that the spores produced on these plants germinate with the spring rains. If regeneration occurs as abundantly under natural conditions as it does in cultures, it seems not impossible that the old thalli thus buried in the spring

may continue their growth by the production of adventitious shoots.

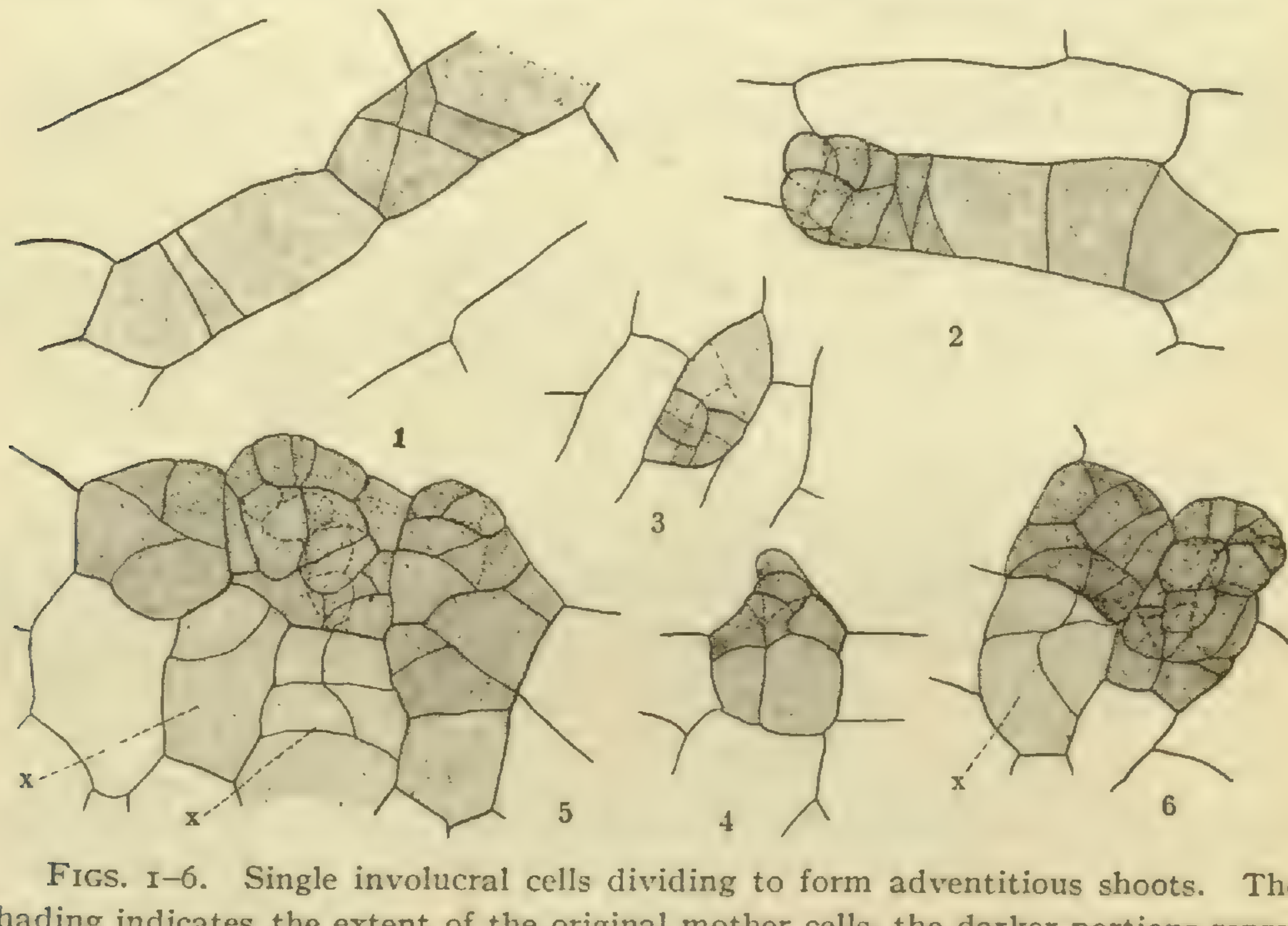
My observations seem to warrant the conclusion that regeneration is a rather common phenomenon in *Sphaerocarpos*, resulting from particular nutritive conditions in the thalli or in parts of the thalli, rather than merely from a direct response to occasional accidental stimuli.

The descriptions that follow are based on data obtained from female plants, these being more abundant and more convenient for study than the male. In a few male plants that were studied, the phenomena observed were similar to those here described. The plants produced by regeneration were in all cases of the same sex as the parent plant. Several cultures of female plants, which were started by sowing involucres separated from the thalli, on soil, are still growing vigorously at the present time, nearly twelve months afterwards, and are still purely female.

In order to study in detail the method of formation of the adventitious shoots, involucres, lobes, and small portions of the midrib were cut off and placed on moist filter paper in petri dishes. At the end of two weeks or thereabouts (in one case after six days), these small pieces of tissue were covered with outgrowths in various stages of development. They were then removed, killed by placing in a dilute solution of chrom-acetic acid (chromic acid, 0.3 g.; glacial acetic acid, 0.7 cc.; distilled water, 99 cc.), stained in eosin, and mounted in glycerin.

When regeneration is about to occur, the contents of a single cell become more dense and richer in chlorophyll content. Such a cell may be isolated, or there may be a group of similar cells adjoining or in close proximity to one another. Cell division then occurs, without an accompanying growth of the mother cell. The relative position of the walls formed in these divisions is quite variable. FIGS. 1, 2, 3, 4, 13, and 14 represent groups of cells formed in this way. It makes no particular difference whether the original cell was on the edge or in the middle of the tissue of the parent plant, nor does its size or shape have any influence on the course of development. Very commonly, indeed in the majority of cases, the walls are set in at acute angles to each other, and in the case of the involucral cells these divisions

occur mostly at one end of the mother cell, the other end being divided into only two or three comparatively large and clear cells (FIGS. 1, 2). The end cell of a row of cells formed in this way suggests a wedge-shaped apical cell, cutting off segments alternately to right and to left. The process is, however, too variable to justify the conclusion that the growth of adventitious shoots is regularly due at first to the activity of such an apical cell.

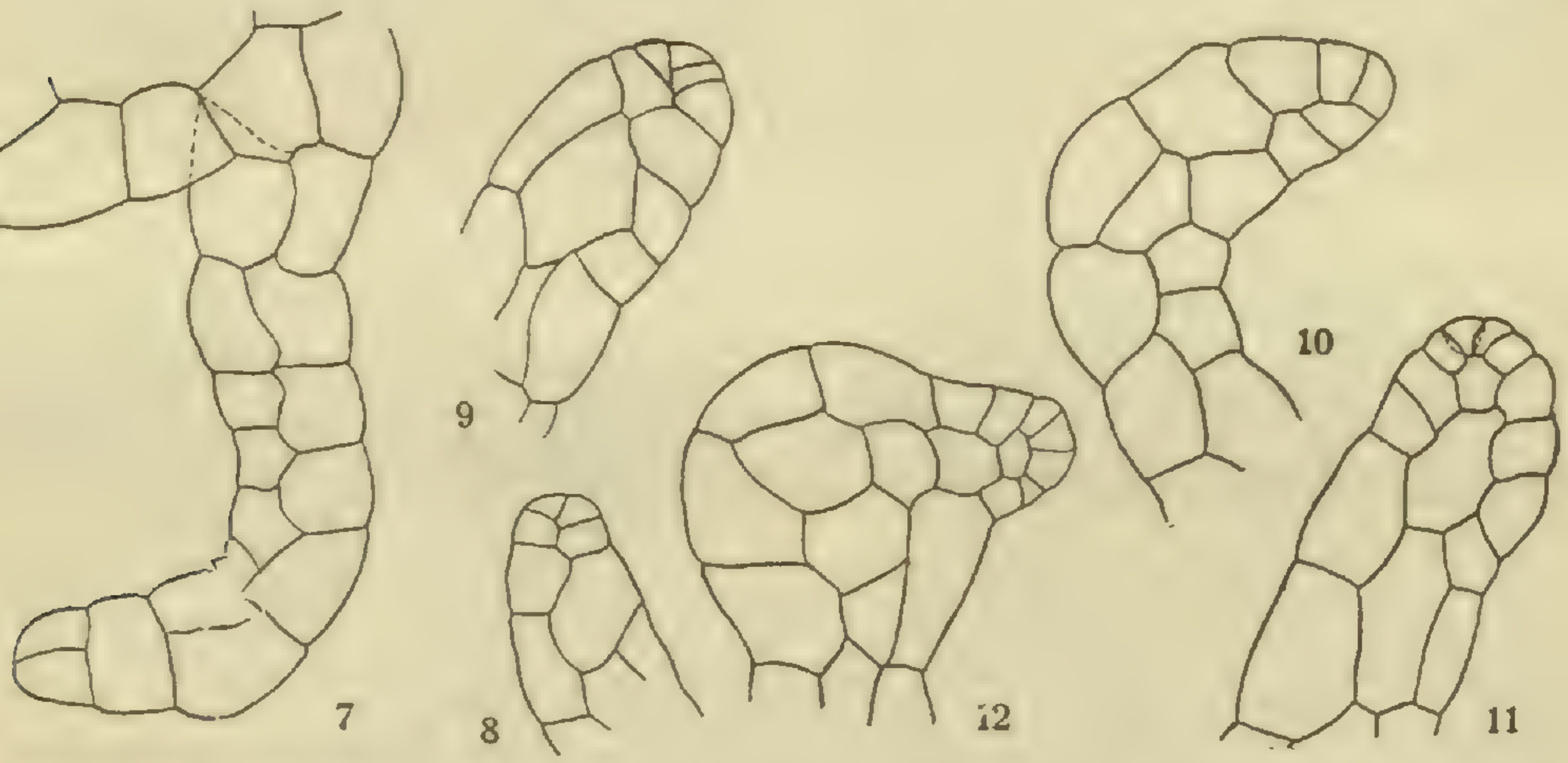


FIGS. 1–6. Single involucral cells dividing to form adventitious shoots. The shading indicates the extent of the original mother cells, the darker portions representing those of the densest contents. FIG. 1. Two adjacent mother cells at an early stage of regeneration. FIGS. 2, 3. The young shoots beginning to project above the surface of the parent tissue. FIG. 4. Shoot arising from a marginal mother cell. FIGS. 5, 6. Shoots arising from adjoining marginal mother cells: *x*, *x*, adjacent involucral cells also dividing. FIGS. 1–4, 6, × 150; FIG. 5, × 200.

As cell division continues, the cell mass so formed begins to protrude above the surface of the parent tissue at one end of the mother cell (FIG. 2). This seems to be due simply to a bulging up of the mass of cells, followed by cell divisions in planes more or less nearly parallel to the surface of the tissue from which the shoot is growing. If regeneration occurs from the margin of the parent tissue instead of in the middle, this bulging out commonly does not occur; the young plant grows straight out from the margin, and gradually curves so as to bring its distal portion into a more erect position.

After the young plant has thus become a distinct outgrowth from the parent tissue, cell divisions occur in many planes, so that there is formed a compact mass of cells several cells thick in each dimension. The form of this mass is globular or cylindrical, and there is no longer any evidence of the existence of an apical cell (FIGS. 5, 6).

The only exceptions found to this history were in the first cases of regeneration noted, mentioned above, in which each young plant grew out as a long ribbon. Presumably this took place by the continuation, after the cell mass had once bulged out from the original containing wall, of divisions similar to those which had cut up the original mother cell. The cell at the tip of



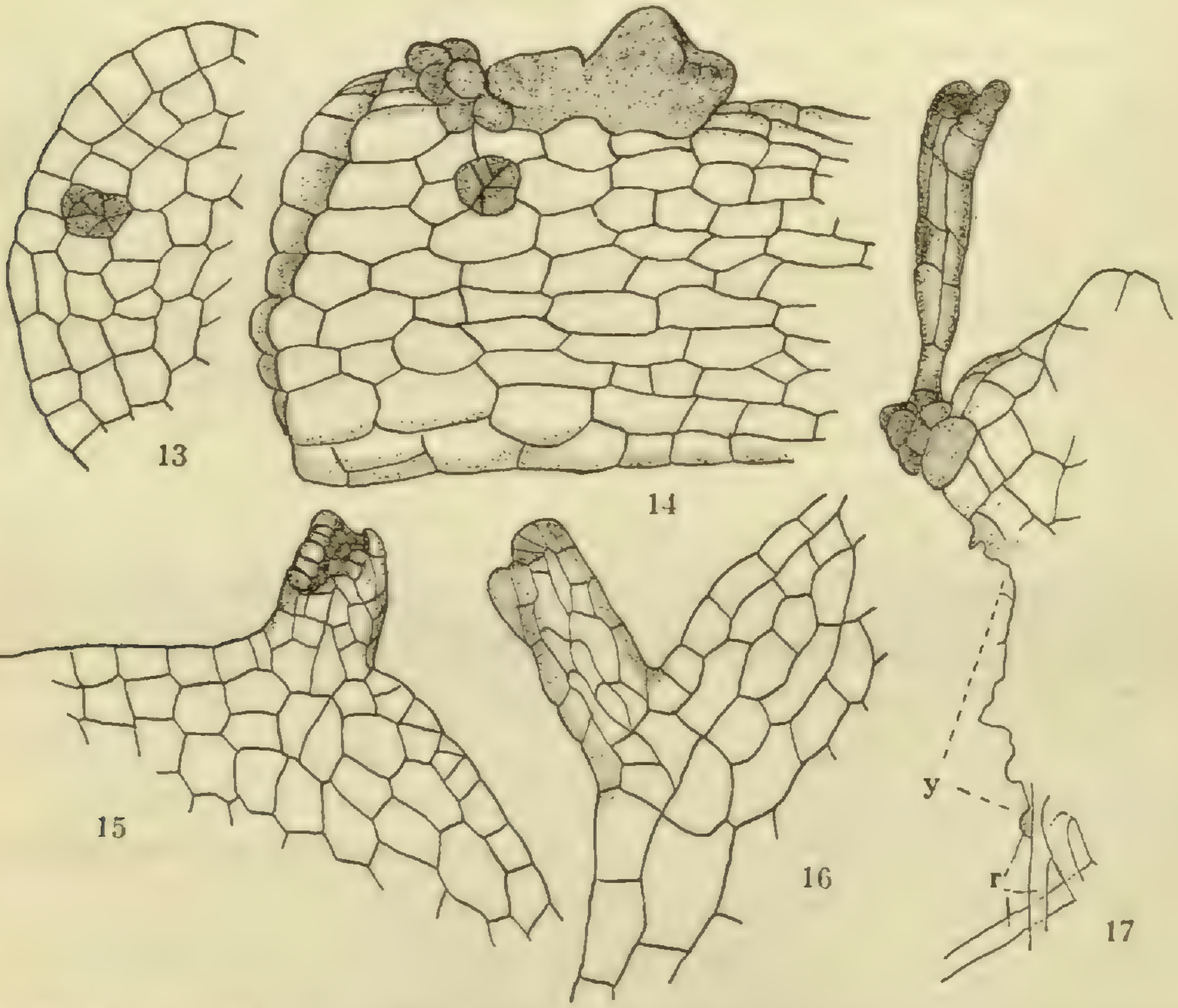
FIGS. 7–12. The tips of filamentous adventitious shoots. FIGS. 8–10. Development by means of a two-sided apical cell. FIGS. 11, 12. Broadening of the apical region into the thallus-plate. All, × 150.

such a ribbon-shaped growth had in most cases exactly the appearance of a two-sided apical cell, cutting off segments alternately to right and to left. The segments themselves redivided only occasionally, so that a narrow shoot, two cells wide and one cell thick, resulted. The tips of such shoots are illustrated in FIGS. 7, 8, 9, 10. These young plants finally broadened out at the tip (possibly in response to more favorable light conditions), and the ordinary flat plate-shaped thallus resulted. As soon as the broadening had occurred, an apical cell could no longer be distinguished, further growth being due to a group of small meristematic cells on the margin of the plate, either in an apical or in a lateral position (FIGS. 11, 12, 19).

This history bears a striking resemblance to that of the sporelings described in a previous paper (5), which developed from spores sown in a nutrient solution. These sporelings were marked by the production of an excessively long germ-tube, which, when conditions were favorable, gradually broadened out into the thallus-plate. In the cases of some sporelings (5, *f. 35*), ribbons were formed which were almost identical in appearance with those just described as arising by regeneration. Obviously the unusual form in each case bears much the same relation to the normal or common method of development. All gradations are found between the two methods among both sporelings and adventitious shoots, the latter, however, being, so far as my observations have shown, by far the more variable.

In cases in which several adjoining cells start regeneration, it seems that the growths produced by each may become fused together into one new plant. This is rather difficult to determine, but it is certain that one often sees many contiguous cells starting to divide, while there are rarely as many plants formed on a single portion of tissue as would represent the development of all these cells into separate plants. The possibilities suggested are that fusion may occur, two or more cell masses growing together into one structure, or that the development of some of these cell masses may be checked. FIG. 14 shows adventitious growths resulting from the division of groups of adjacent cells. In FIGS. 15, 16, and 19, the young plants seem to have developed each from a single marginal cell of a lobe, the base of the shoot not being much wider than a single marginal cell. FIG. 18 represents several plants arising by regeneration from the margin of the opening of an involucre. Here also each plant seems to have developed from a single cell. FIGS. 5 and 6 show similar groups of marginal cells at an earlier stage in regeneration. The cell masses resulting from the division of individual marginal cells can be fairly readily distinguished, and seem to be each in process of forming independent shoots; but there are other cells (*x*) adjoining these which have also divided, and it is impossible to say whether the cell groups thus formed will also give rise each to a separate plant or whether they will merely contribute to the cell masses formed from the marginal cells.

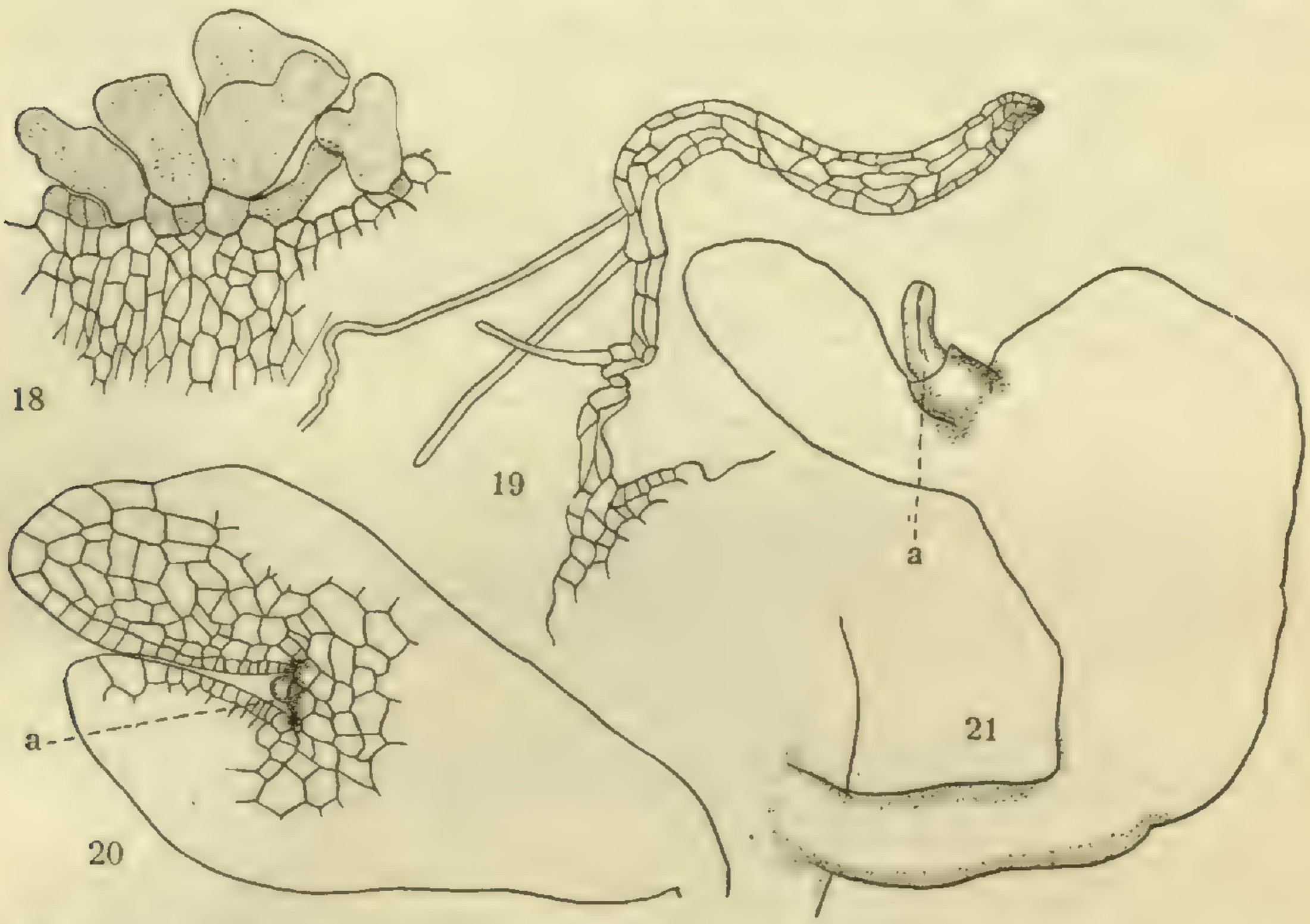
Very often, the surrounding cells being largely dead or dying, the cells which form the new plants assume a globular form and stand out from the surrounding tissue. This is especially true when regeneration occurs from the midrib. Such a case is shown in FIG. 17. Here also there is a strong suggestion that a group of cells is concerned in the production of a single new plant.



FIGS. 13–17. The further development of shoots produced by regeneration from involucres and lobes. The shading indicates the density of the cell contents in the new plants. FIG. 13. Regeneration from a single cell of a lobe. FIG. 14. Cell masses produced by the division of a number of adjoining mother cells of an involucre. The cell contents were so dense that the cell walls could not be distinguished. FIGS. 15, 16. Regeneration from the margins of lobes. FIG. 17. Regeneration from the midrib: *y*, cut surface; *r*, rhizoids. All drawn from living material, × 75.

In the course of the usual history, after the young plant has developed into a small globular or cylindrical mass, a flat plate is formed as the result of the continued division of a group of cells at the tip of the structure. FIGS. 15 and 16 represent cases in which this process is taking place at an early stage; in FIGS. 17, 21, 22, and 23 the original cell mass has developed into a long and

comparatively slender body, in one case (FIG. 17) strongly suggestive of the germ-tube formed as a result of spore germination. As in the latter process, the thallus-plate is at first usually cup-shaped or trough-shaped (FIG. 15), and the growing point may lie in a median or in a lateral position. The tissues formed to right and left of the apical point grow rapidly, so that the latter lies at the base of a deep apical notch (FIGS. 20, 21, 22). As in the case of the sporeling, the first sex organ appears very early



FIGS. 18–21. Young plants produced by regeneration. FIG. 18. Shoots arising from a number of adjoining marginal cells of the involucre. The cellular structure of the shoots is not shown. FIG. 19. Filamentous shoot produced from the margin of a lobe. FIG. 20. The terminal plate of a young plant, showing the apical notch: *a*, young archegonium. Fig. 21. Young shoot, consisting of a cylindrical basal portion and a terminal flat plate: *a*, archegonium enclosed in young involucre. FIGS. 19–21 drawn from living material. Figs. 18, 19, × 35; FIGS. 20, 21, × 75.

(FIG. 21), being formed immediately behind the growing point. Presumably an apical cell, or group of initials, is developed in the growing region just previous to the formation of the first sex organ, since from this point the history of the adventitious shoot is identical with that of a typical thallus (5).

In the case of some of the male plants studied, the young plant arising by regeneration produced only a few antheridia,

and assumed a very elongated form, with few lobes. Such a plant is shown in FIG. 23. Similar results were obtained from female plants by allowing regeneration to occur under water (FIGS. 24, 25). In one case (FIG. 24), no sex organs were produced, and scarcely any lobes. In another case (FIG. 25), the tip of the plant reached the surface of the water and there began to take on

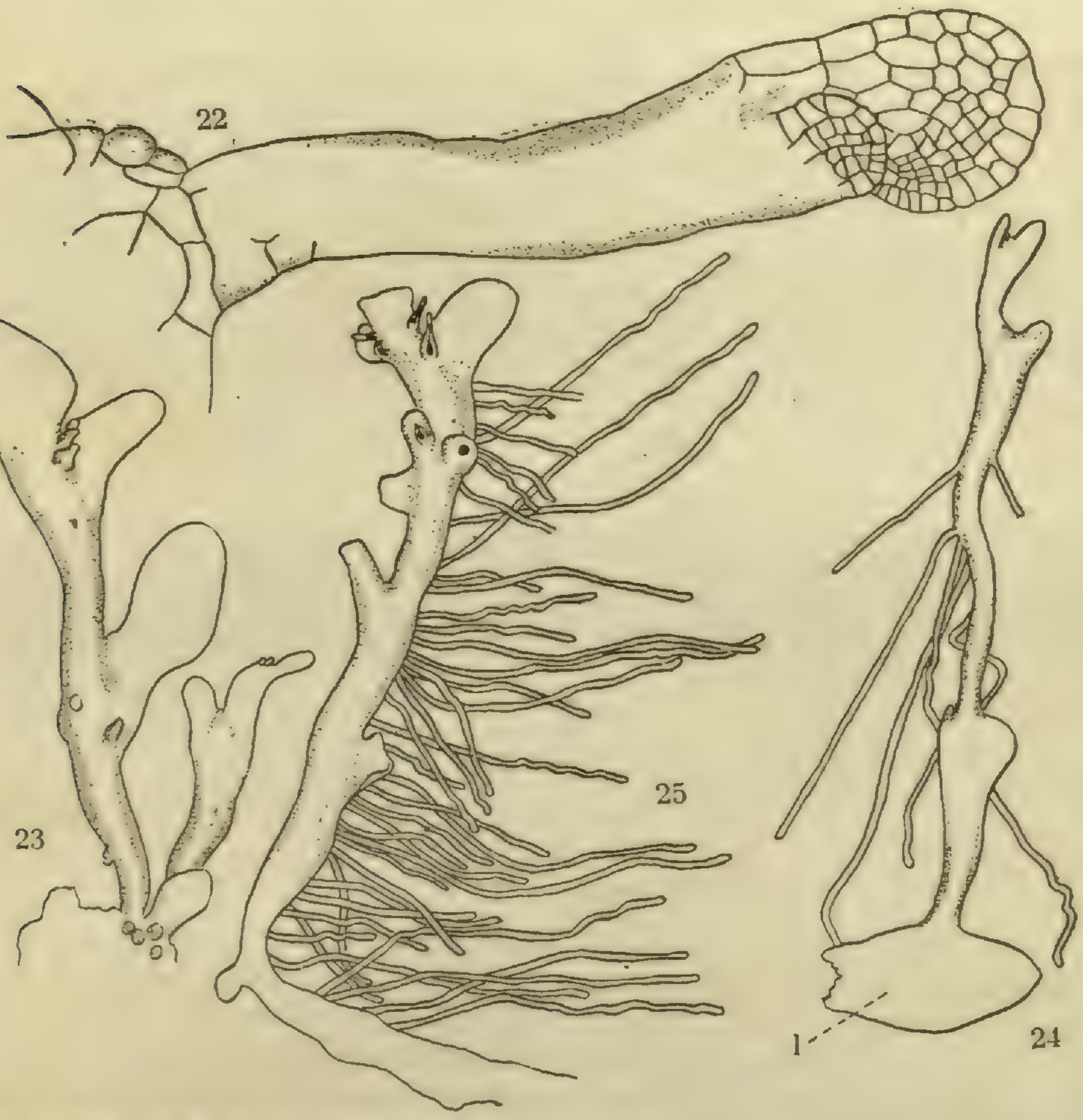


FIG. 22. The apical notch formed laterally on a long cylindrical cell mass. FIG. 23. Young plant, with antheridia, produced by regeneration from the lobe of a male plant. FIGS. 24, 25. Shoots developed from portions of female plants cultivated under water: *l*, parent lobe. All drawn from living material. FIG. 22, × 100; FIGS. 23–25, × 20.

more nearly the ordinary appearance. Production of rhizoids was especially abundant in this latter case.

SUMMARY

1. Regeneration in *Sphaerocarpos Donnellii* may occur from any vegetative tissue of the thallus, either when the thallus as a

whole is partly dead, or when portions of it are separated or partly separated from the rest under conditions favorable for growth.

2. Plants produced by regeneration originate for the most part in a single cell, which divides irregularly to form a cell mass whose shape is dependent on environmental conditions. It is possible that in some cases this cell mass may originate from several adjoining cells of the parent plant instead of from one cell only.

3. There is a tendency towards the formation of a two-sided apical cell in the early stages, this being most marked when conditions are comparatively unfavorable. This tendency may lead to the formation under unfavorable conditions of a long, narrow, ribbon-shaped plant.

4. The development of the first cell mass, globular, cylindrical, or ribbon-like, into a typical thallus takes place in a manner entirely analogous to the development of a mature thallus from the germ-tube produced by a spore on germination.

DEPARTMENT OF BOTANY,
UNIVERSITY OF WISCONSIN

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A misconception as to the structure of the ear of maize

PAUL WEATHERWAX

(WITH SIX TEXT FIGURES)

It is a fact of common knowledge and general interest that the rows of an ear of corn regularly occur in even numbers. By the layman this has usually been regarded as one of Nature's curiosities, not necessarily to be explained in any way; but the botanist long ago found it to be the expression of a morphological characteristic of the whole tribe (Maydeae) to which maize belongs.

Ordinarily the spikelets in all parts of both inflorescences of the maize plant are borne in pairs, one sessile and the other pedicelled. The fundamental structural unit of the ear of corn is a row of these paired spikelets, or, in other words, a pair of rows of grains, each spikelet producing one grain. As a rule there is no ascertainable difference between the two grains produced in a pair of spikelets, but there is abundant evidence that the sessile spikelets are responsible for one row and the pedicelled ones for the other.

It often happens that an ear has more rows at the base than at the tip, the difference in number being always two or a multiple of two. When the difference in number is two, both rows are dropped at exactly the same distance from the base of the ear; if the difference is more than two, two rows may be dropped at one distance from the end of the ear, two at another, and so on. Thus, no part of the ear is ever left with an odd number of rows.

The natural inference has been that these irregularities are due to the discontinuance of one or more rows of paired spikelets, an explanation apparently in harmony with most facts and theories centered in this unique structure. It is somewhat surprising, therefore, to find in connection with a recent theory* as to the origin of the ear of maize, a new explanation of this irregularity in the rows.

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* Collins, G. N. Structure of the maize ear as indicated in *Zea-Euchlaena* hybrids. Jour. Agr. Research **17**: 127–135. *pl. 16–18 + f. 1.* 1919.

FIG. 1. An ear with eighteen rows at the base and ten at the tip.

A cardinal point in Collins's new theory of the origin of the ear is that each pair of spikelets is yoked structurally with another pair on the opposite side of the ear; and the statement is made (pp. 133–134) that a reduction in the number of rows between the base and the tip of the ear is due not to the discontinuance of a row of pairs of spikelets, but to the loss of the pedicelled spikelets from yoked pairs for a part of the length of the ear. No criticism of the general bearing of the theory is intended here, but the corollary statement as to the manner of the loss of rows cannot go unchallenged.

Just what technique was employed in securing this anomalous bit of evidence is not explained, except that many ears are said to have been examined, and reference is made to tassels having pistillate portions. In external appearance, an ear of corn is a very deceptive thing, and peculiar technique is sometimes necessary to bring out its true structure. The semblance of rows on the surface, being largely due to the adjustment of crowded units to their allotted space, may often be more properly regarded as geometrical rather than morphological, especially when any structural peculiarity is concerned (FIG. 1).

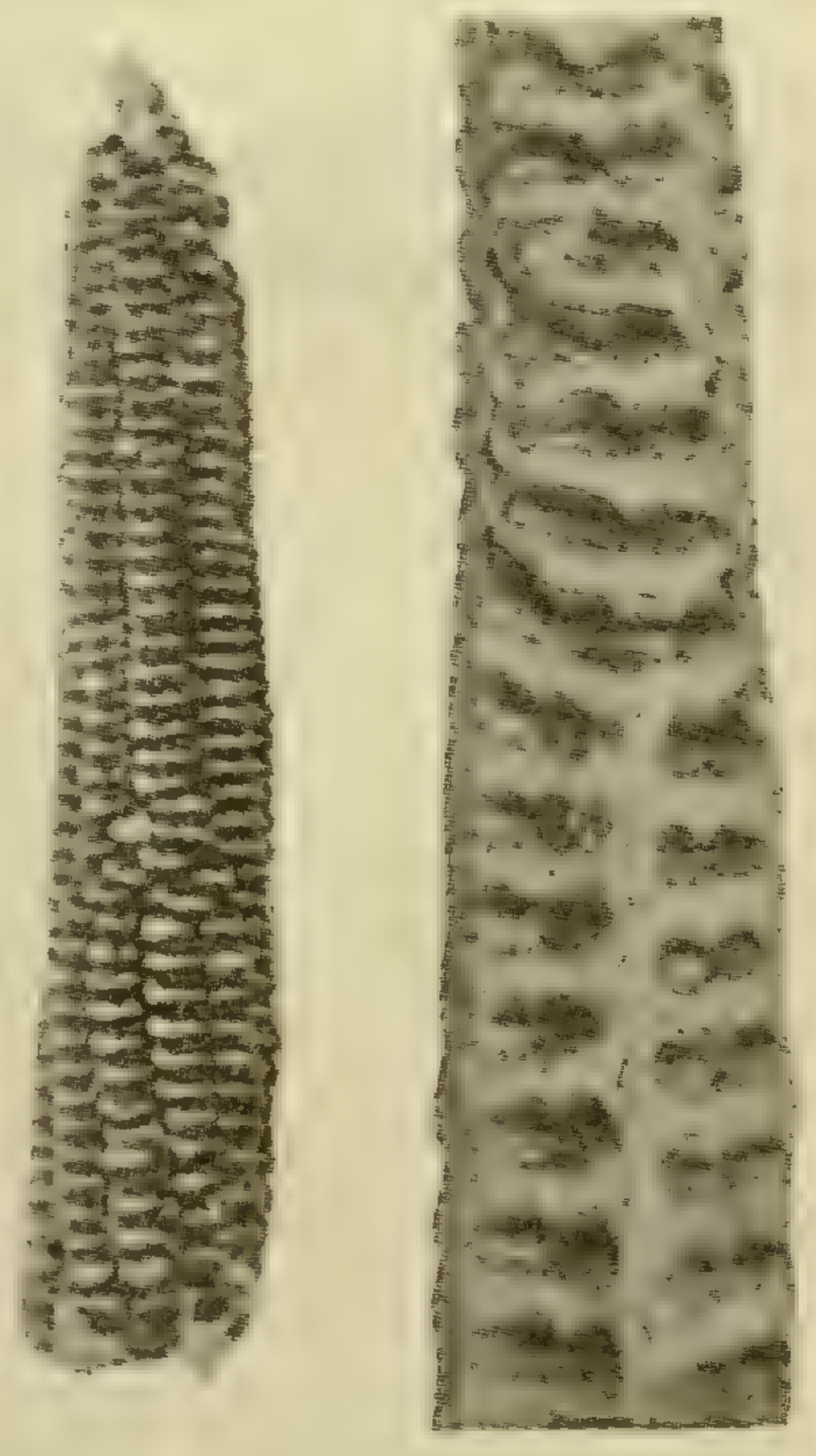

FIG. 2. An ear of corn with ten rows at the base and eight at the tip, × ½. FIG. 3. The cob of the ear shown in FIG. 2, after treatmentas described in the text, × 1⅛.

A reliable technique to bring out the arrangement of the spikelets, when any irregularity is evident, may be borrowed from the maker of corncob pipes. The first step in the process, after the removal of the kernels, is to shave off with a sharp knife the chaff on the outside of the cob.

This chaff consists of the glumes and palets of the spikelets, and its removal exposes the alveoli, in each of which a pair of spikelets is borne. When these alveoli are brought out clearly, the work may be finished with a piece of sandpaper, but this is usually unnecessary. Any corncob, typical or anomalous, when treated in this way, displays a number of longitudinal series of alveoli corresponding to the rows of paired spikelets.

The results secured when this method is applied to an ear having more rows at the base than at the tip are best explained by reference to the figures. Fig. 2 is an ear of flint corn with ten rows at the base and eight at the tip; four rows are seen apparently giving place to two near the middle of the ear. If this change occurs as Collins explains it, we should find on the cob of this ear five rows of alveoli running full length; but FIG. 3, which shows a portion of the cob of this ear treated as above described, shows the fallacy of this theory. There are five rows of alveoli at the base and four at the tip, the change in number occurring at the exact point where two rows of grains are dropped. These results were duplicated with several ears, no ear being found

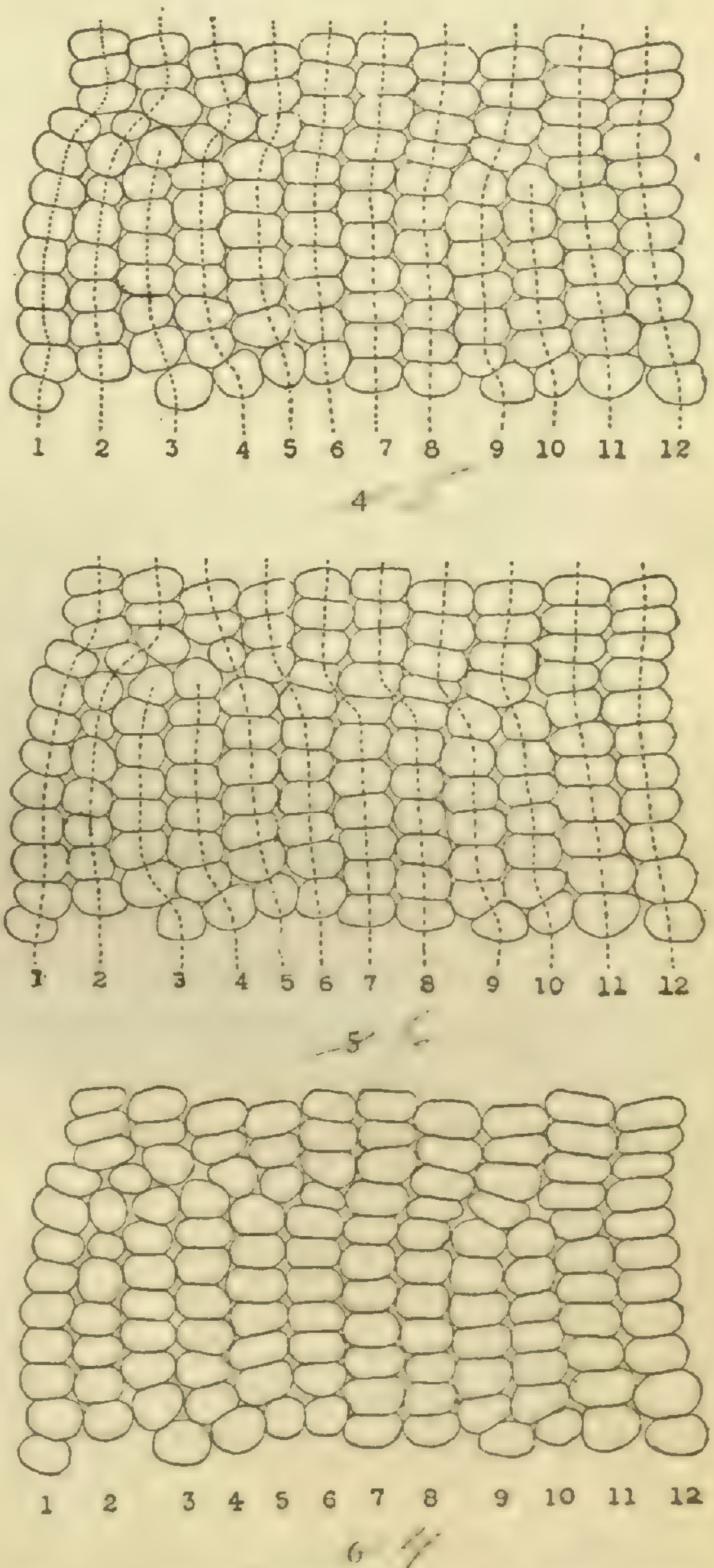

FIG. 4. Transition from twelve to ten rows.
FIG. 5. The erroneous explanation of FIG. 4; the dotted lines indicate the continuity of rows.
FIG. 6. The correct explanation of the transition indicated in FIG. 4.

that gave contrary results; particularly striking results were obtained with an ear having ten rows at one end and eighteen at the other (FIG. 1). The evidence is conclusive that the difference in number of rows is due to the discontinuance of a row of pairs of spikelets and not to the abortion of the pedicelled spikelets of two such rows.

FIGS. 4–6 show, in a composite camera lucida drawing, a belt around an ear, covering the point of transition from twelve rows to ten. The structure of the ear shows that 1 and 2, 3 and 4, 5 and 6, etc., are respective pairs of rows. FIG. 5 shows Collins's interpretation of the loss of rows, if this is a case where the location of rows can be determined with what he calls "reasonable certainty" (p. 134); rows 3 and 10, representing the pedicelled spikelets of their respective pairs, are dropped. But the method here described removes all doubt and is applicable to all ears regardless of their external aspect. It shows, as in FIG. 6, that the two rows lost constitute one pair.

It is probably incorrect to speak of the "loss" of rows except as an event incident to our progress in examing the ear from one end to the other, for the actual *loss* of rows in this case is probably not a fact of either phylogeny or ontogeny. There is nothing to indicate that the short rows represent long rows partially aborted. In fact the abortion of spikelets or of rows in the ear seems to be much more constant as a characteristic of theories demanding it for consistency than of real ears of corn; and the integrity of the pair of pistillate spikelets seems to be maintained quite as constantly in maize as is the abortion of one of the pair in teosinte.

UNIVERSITY OF GEORGIA,
ATHENS, GEORGIA

INDEX TO AMERICAN BOTANICAL LITERATURE

1919–1920

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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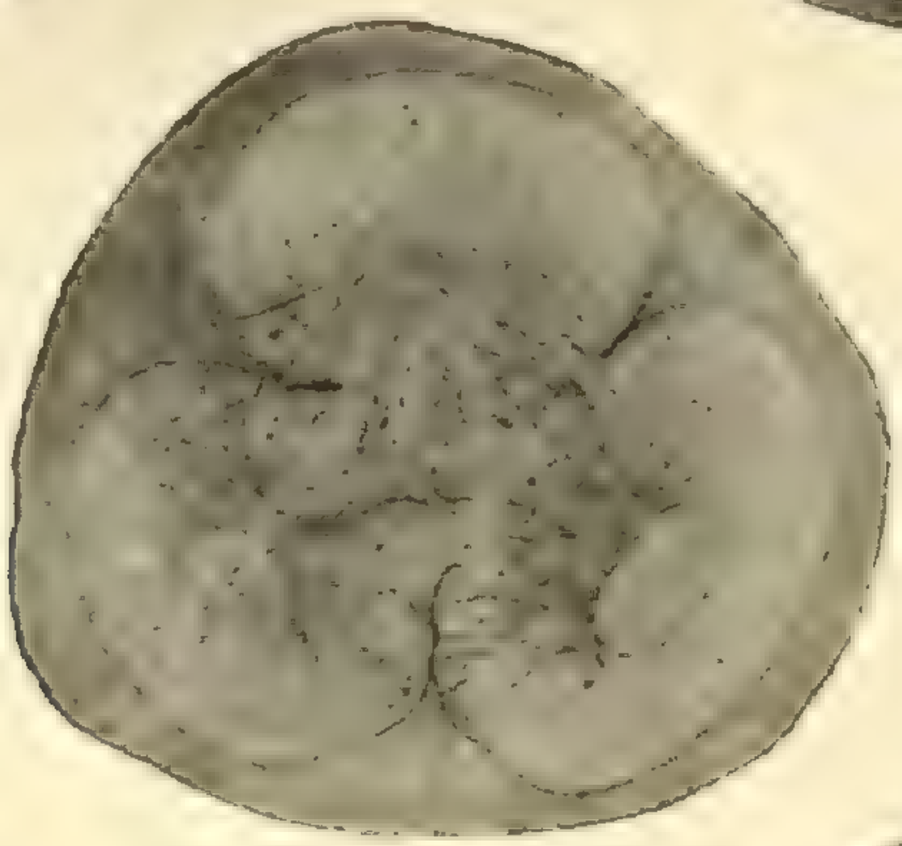

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FARR: POLLEN-MOTHER-CELL OF COBAEA

Vol. 47 No. 9

BULLETIN

OF THE

TORREY BOTANICAL CLUB

SEPTEMBER, 1920

Calymperaceae of North America

R. S. WILLIAMS

(WITH PLATES 15–17)

The next part of the North American Flora relating to mosses will comprise the families Fissidentaceae and Calymperaceae. The second of these families includes only two genera, *Syrrhopodon* and *Calymperes*. The results obtained from the study of this group are here offered in advance, partly to allow the illustrations of cross-sections of the leaves to be issued with the descriptions.

SYRRHOPODON Schwaegr. Suppl. 2²: 110. 1824

Dioicous or rarely autoicous. Growing in mostly compact cushions of pale green to greenish brown color with more or less radiculose, branching stems from a few millimeters to 6–8 cm. high. Leaves with mostly imbricate, often conspicuously white base, mostly narrowed upward to a point varying from straight to crispate and from lanceolate to lingulate or ligulate, with acute or rounded, mostly denticulate apex and having a distinct border (except in *S. martinicensis*) either much thickened or of hyaline or yellowish cells. Costa stout, from nearly percurrent to excurrent, often papillose or spiny on one or both sides, in cross-section showing one row of guide-cells with rarely a few accessory guide-cells, stereid bands above and below them and outer cells mostly differentiated. Leaf-cells throughout upper part of leaf chlorophyllose and roundish or oval to quadratic, rarely smooth, mostly papillose or mamillose on one or both sides; cells of the erect base mostly hyaline (the cancellinae), square to linear, changing abruptly into the green cells of upper part of leaf. Perichaetial leaves usually smaller than the stem-leaves. Seta erect, elongate

[The BULLETIN for August (47: 325–366. *pl. 14*) was issued October 5, 1920.]

and smooth. Capsule erect, regular, oval to cylindric, mostly smooth and glossy. Annulus none. Peristome-teeth rarely wanting, mostly narrowly lanceolate and undivided, sometimes very short and irregular, usually papillose and golden brown. Lid conical and often long-rostrate. Calyptra cucullate, the base entire or somewhat split, the apex often rough. Spores usually rough. Gemmae often borne on the leaves, either growing from the upper costa or rarely from cells of leaf-blade on either side of the costa. [PLATES 15, 16.]

Type species: *Calymperes Gardneri* Hook.

Leaf-margin with external cells not differing in color or length from those of blade within but sometimes with an inner stereid band.
Margin much thickened, forming a distinct border.
Border triangular in cross-section and more or less doubly serrate-winged.
Leaf-base golden brown or reddish.
Leaves less than 0.4 mm. wide and about 1 mm. long, the margin sharply dentate with often spreading somewhat ciliate teeth. 1. *S. rigidus.*
Leaves mostly over 0.8 mm. wide and about 1.5 mm. long, the margins slightly serrulate above. 2. *S. Bernoullii.*
Leaf-base mostly pale or hyaline.
Costa very rough with papillae up to 8 mm. high, more prominent on the back in the lower than the upper half of costa. 3. *S. floridanus.*
Costa nearly smooth or much smoother on the back in the lower half than in the upper half, with papillae up to 4 mm. high. 4. *S. incompletus.*
Border oval in cross-section, not winged and distantly serrulate; cells throughout upper leaf, distinct, mostly oval. 5. *S. Berterianus.*
Margin not thickened, without a border. 6. *S. martinicensis.*
Leaf-margin with hyaline or yellowish border of narrow, elongate cells (sometimes wanting in upper part of leaf), sharply defined from cells of blade within.
Border of a mostly cylindric band of stereid cells extending from or near apex to the basal part.
Margin entire or nearly so all around except at apex of leaf.
Leaves with point crispate when dry and only one or two times longer than the broadened leaf-base.
Costa smooth on both sides except at the denticulate apex; leaf-cells densely covered with low papillae. 7. *S. Gaudichaudii.*
Costa more or less spiny dentate on back to

below the middle; leaf-cells with often high, spine-like papillae. 8. *S. inflexus.*

Leaves with point spreading-flexuous to incurved or nearly straight when dry and from two to many times longer than the basal part, or without a distinctly broader basal part.

Costa without accessory guide-cells; stems usually much longer than the longest leaves (about 12 mm.)

Leaves rather distant with the point abruptly spreading from the conspicuous, appressed base; costa dentate at apex, not papillose below. 9. *S. Husnoti.*

Leaves closer together on the stem with less spreading points; costa mostly papillose on the back in the upper part as well as dentate at apex. 10. *S. flavescens.*

Costa with accessory guide-cells; stems much shorter than the longest leaves (stems usually 5–6 mm. long and leaves up to 4 cm. long). 11. *S. tenuifolius.*

Margin serrulate to enlarged base, or base with more or less serrate or spiny-dentate border.

Cells of leaf smooth. 12. *S. lycopodioides.*

Cells of leaf either mamillose or papillose, that is, similar on both sides.

Costa about 25 μ wide halfway up, smooth except near the apex. 13. *S. recurvulus.*

Costa 50 μ wide or more half way up.

Smooth or with minute, distant teeth on the back, the upper face papillose mostly from just above the cancellinae half way to apex. 14. *S. graminicola.*

Rough with prominent, often spine-like teeth on the back.

Costa spiny-dentate on the back in the upper half, otherwise smooth. 15. *S. elongatus.*

Costa with dense, compound or forking papillae extending to below the cancelinae on the back. 16. *S. texanus.*

Border mostly wanting in upper third of leaf or in some leaves scarcely present or entirely wanting throughout.

Cancellinae mostly broad and somewhat rounded above. 17. *S. ligulatus.*

Cancellinae terminating above in narrowly acute angles next the costa.

Costa near the apex of cancellinae 60–80 μ wide and leaf-blade 0.6–1 mm. or more wide. 18. *S. parasiticus.*

Costa near apex of cancellinae 40–50 μ wide and leaf-blade 0.25–0.50 mm. wide. 19. *S. filigerus.*

1. SYRRHOPODON RIGIDUS Hook. & Grev. in Brewster, Edinb. Jour. Sci, 3: 226. 1826

Calymperes androgynum Mont. Ann. Sci. Nat. II. 3: 195. 1835.
Syrrhopodon longisetaceus C. Müll. Syn. 1: 535. 1849.

Dioicous, male plants much like the fertile in habit, bearing several buds in the axils of the upper leaves rather over 1 mm. long, composed of two or three broadly ovate, lanceolate-pointed, serrulate and costate perigonial leaves, enclosing eight to ten antheridia about 0.5 mm. long, with few paraphyses: in rather compact, dull, brownish green cushions, red-tomentose within, with stems 1–3 cm. high; stem-leaves 7–8 mm. or sometimes up to 12 mm. long, spreading flexuous, from an ovate base 1–1.5 mm. long, with margins sharply serrulate or somewhat spiny-dentate with often spreading teeth, rather gradually narrowed to a linear-lanceolate, acute point up to seven or eight times longer, with thickened, doubly serrate borders; costa stout, excurrent, grooved, enlarged at apex and bearing numerous slender propagula with two or three cross-walls, smooth in lower part, mostly rough above on both sides or rarely nearly smooth, in cross-section showing about seven guide cells, large stereid bands above and below and outer cells differentiated all round; cells throughout upper part of leaf distinct, mostly oblong, 6–8 μ wide and 12–16 μ long, mamillose on upper side, smooth beneath; cancellinae not filling entire basal part of leaf, more or less golden or reddish brown, mostly terminating above in acute angles; perichaetial leaves about like upper stem-leaves, but the inner smaller; seta 2–2.5 cm. long; capsule oblong, about 1.7 mm. long with conical, rostrate lid of about equal length; peristome a low, yellowish membrane, when moist scarcely extending above rim of capsule; spores rough, up to about 22 μ in diameter; calyptra nearly smooth throughout. [FIG. 1.]

TYPE LOCALITY: Trinidad.

DISTRIBUTION: Porto Rico, Guadeloupe, Martinique, St. Vincent, Grenada, Trinidad and northern South America.

ILLUSTRATION: Ann. Sci. Nat. II. 3: *pl. 3, f. 2.*

2. SYRRHOPODON BERNOULLII C. Müll. Bull. Herb. Boiss. 5: 189. 1897

Syrrhopodon Pittieri Ren. & Card. Bull. Soc. Bot. Belg. 41[1]: 54. 1905.

Dioicous, male plants stout, branching, with often abundant axillary flowers, the perigonial leaves mostly golden brown, the

inner ovate, acute, not quite entire, the outer longer with pale, lanceolate, serrulate point, enclosing five or six antheridia a little over one half mm. long with somewhat longer paraphyses: in large, not very compact, greenish brown tufts, with more or less curved, branching stems, tomentose below, up to 4 or 5 cm. high; stem-leaves spreading-flexuous, up to 6 or 7 mm. long, from an oblong-ovate, mostly golden brown base about 1.5 mm. long, slightly crenulate or serrulate on borders, gradually narrowed to a linear-lanceolate point, tubulose when dry, with thick, doubly serrate margins and acute apex; costa not quite percurrent, serrulate on back toward apex, smooth below, one half up about one sixth the width of leaf, in cross-section showing six or seven guide cells, large stereid bands above and below and outer cells differentiated; leaf-margin in cross-section triangular, showing a stereid band surrounded by rather large outer cells; cells throughout upper leaf mostly slightly elongate, the median about 6 μ wide by 7–8 μ long; cancellinae filling a rather small part of leaf-base, mostly broad and rounded or truncate above; inner perichaetial leaves scarcely smaller than outer; seta 10–18 mm. long; capsule ovate-oblong, small-mouthed, about 2 mm. long with a slender-beaked lid 1.5 mm. long; peristome teeth projecting above the mouth about 75 μ, often united to near apex, rather pale, with often numerous, golden brown, wart-like projections over the outer surface; spores rough, 18–24 μ in diameter; calyptra rough near apex. [FIG. 2.]

TYPE LOCALITY: Guatemala.

DISTRIBUTION: Guatemala to Panama and in Guadeloupe (*Père Duss 631*).

3. SYRRHOPODON FLORIDANUS Sull. in Gray, Man. ed. 2, 631. 1856

Dioicous: in compact cushions, greenish brown above, rusty brown within, with more or less fasciculate branching stems, somewhat tomentose below, up to 3 cm. high; stem-leaves incurved or crispate when dry, the upper 4.5–5 mm. long, from an ovate base about 1 mm. long, somewhat narrowed to a nearly linear point three and one half to four times longer with incurved, doubly serrulate-lamellate borders and broadly acute or obtuse, serrulate apex; costa not quite percurrent, about 80 μ wide half way up the leaf, mostly densely covered on the back, from the middle to the broadened base of leaf, with high, almost spine-like, papillae; leaves in cross-section near middle showing a terete costa with five or six guide-cells, large stereid bands above and below and outer cells differentiated; leaf-blade with cells highly mamillose on upper side, nearly smooth or somewhat mamillose

on under side with a leaf-border triangular in cross-section, of about eight cells sometimes enclosing one or two stereid cells; cells of upper blade distinct, mostly somewhat angular, scarcely elongate, 5–7 μ in diameter; cancellinae extending up about 1 mm. from base, mostly rounded, sometimes acutely angular at apex; perichaetial leaves scarcely differing from those of upper stem; pedicel erect, 7–8 mm. long; capsule ovate-cylindric, about 1.75 mm. long, the flattish lid with acicular beak rather shorter; peristome-teeth attached well below the mouth, somewhat irregular, short-lanceolate, pale, projecting above the rim 50–60 μ, with five or six articulations; spores rough, about 16 μ in diameter; calyptra slightly rough above. [FIG. 3.]

TYPE LOCALITY: Florida.

DISTRIBUTION: Florida, Alabama, Georgia and Bermuda.

ILLUSTRATION: Sull. Icon. Musc. *pl. 31*.

This is very close to the next species, but the costa is usually much rougher on the back, and the cells of the upper part of the leaf are less inclined to be slightly elongate.

4. SYRRHOPODON INCOMPLETUS Schwaegr. Suppl. **2**[1]: 119. 1824

Syrrhopodon Hobsoni Hook. & Grev. in Brewster, Edin. Jour. **3**: 224. 1824.

Syrrhopodon semicompletus Schwaegr. Suppl. **2**[2]: 97. 1827.

Calymperes Hobsoni Grev. Ann. Lyc. N. Y. **1**: 271. 1825.

Syrrhopodon Mohrii C. Müll. Linnaea **38**: 633. 1874.

Syrrhopodon brachystelioides C. Müll. Nuovo Giorn. Bot. Ital. II. **4**: 48. 1897.

Syrrhopodon decolorans C. Müll. Bull. Herb. Boiss. **5**: 188. 1897.

Dioicous, male flowers one to several, terminal and axillary, the inner perigonial leaves short, broadly ovate, acutish, costate, minutely serrulate, nearly or quite without green point, enclosing numerous antheridia and paraphyses a little over 0.5 mm. long: in extensive, brownish green mats with more or less curved and branching stems 1–5 cm. long; stem-leaves 4–5 mm. long, from a rather broad, ovate or obovate base serrulate on margins above, abruptly narrowed to a broadly linear, when dry often subtubulose, point with thickened doubly serrulate border extending to the broadly acute or somewhat rounded serrulate apex; costa not quite percurrent, 60–70 μ wide one half up leaf and about one sixth leaf-width, at apex denticulate, below from nearly smooth on both sides to more or less papillose (the papillae mostly 1–4 high) on back down to cancellinae, in cross-section showing about

six guide cells with stereid bands above and below and outer cells differentiated; cells throughout upper part of leaf from nearly square to hexagonal, often slightly elongate, the median mostly 5–6 μ wide and 6–8 μ long, mamillose on upper side, smooth or slightly mamillose or papillose on under side; cancellinae filling two thirds to three fourths of the leaf-base, broad and rounded above; inner perichaetial leaves very similar to outer but smaller; seta 6–7 mm. long; capsule oblong-ovate, small-mouthed, rather over 2 mm. long without lid, the beaked lid about two thirds as long; peristome a rather pale, smoothish membrane not extending above the mouth, often nearly entire; spores rough, 16–18 μ in diameter; calyptra slightly rough above. [FIG. 4.]

TYPE LOCALITY: Cuba.

DISTRIBUTION: Mexico, Florida, Cuba, Jamaica, Porto Rico, Montserrat and Guiana, South America.

ILLUSTRATION: Schwaegr. Suppl. 2: *pl. 180.*

EXSICCATI: Krypt. Exsic. Mus. Palat. Vindob. *1896*, as *Syrrhopodon Hobsoni.*

5. SYRRHOPODON BERTERIANUS (Brid.) C. Müll. Syn. 1: 539. 1849

Dicranum Berterianum Brid. Bryol. Univ. 1: 445. 1826.
Syrrhopodon laevidorsus Besch. Rev. Bryol. 18: 75. 1891.

Apparently dioicous, male flowers not found: in rather loose, deep, brownish green tufts with stout stems up to 7–8 cm. high; stem-leaves 5–6 mm. long, from a broad, obovate, erect and clasping base, slightly serrulate on margins above, abruptly narrowed to a linear, spreading-flexuous point with acute apex and thickened, distantly serrulate borders; costa not quite percurrent, nearly one third the width of upper leaf, terete, smooth on both sides; leaf in cross-section showing about six guide-cells in costa with large stereid bands above and below and outer cells differentiated all round, the leaf-border of a small stereid band enclosed by larger outer cells; cells throughout upper part of leaf distinct, mostly oval, 6–8 μ wide by 8–12 μ long, smooth on under surface, mostly mamillose above; cancellinae filling one half to two thirds of leaf-base, broad and rounded or truncate above; perichaetial leaves very similar to stem-leaves; seta 10–13 mm. long; capsule oblong, up to 2.5 mm. long with conical, slender-beaked lid two thirds as long; peristome not seen; calyptra smooth; spores rough, spores rough, up to 16 μ in diameter. [FIG. 5.]

TYPE LOCALITY: Porto Rico.

DISTRIBUTION: From Cuba and Jamaica to Trinidad and northern South America.

6. SYRRHOPODON MARTINICENSIS Broth. Symb. Ant. 3: 422. 1903

Flowers and fruit unknown: in dull green cushions with stiff, erect stems 2–2.5 cm. high, in cross-section showing two to four rows of outer, thick-walled, golden brown cells and no central strand; stem-leaves 3.5–4 mm. long and 1 mm. wide, when dry obliquely incurved or appressed-imbricate, forming a compact bud at apex of stem showing the conspicuous, glossy, whitish costae, the leaf either oblong-ovate or slightly obovate, the base more or less yellowish; leaf-margin incurved when dry, not thickened, papillose on border, otherwise entire or slightly denticulate at apex; costa percurrent, broad and yellowish at base, about 300 μ wide and one third the width of leaf, tapering gradually to apex, in cross-section near middle showing about seven guide-cells with stereid bands above and below of about equal size and outer cells scarcely or not differentiated; cells throughout upper part of leaf more or less hexagonal, scarcely elongate, on upper side mostly mamillate and unipapillate, on under side papillate; cancellinae of leaves growing from below the apex of stem distinct, broad, extending about one third up leaf and terminating in rather acute angles; cancellinae of inner leaves at apex of stem rather ill-defined and leaf-cells on either side of costa just above the cancellinae mostly covered with a dense, green mass of filiform propagula up to 0.8 mm. long, with twenty-five cross-walls. [FIG. 6.]

TYPE LOCALITY: Martinique.

DISTRIBUTION: Guadeloupe and Martinique.

7. SYRRHOPODON GAUDICHAUDII Mont. Ann. Sci. Nat. II. 2: 366. 1845

Dioicous, male plants about like the fertile, with often several antheridial buds aggregate near the apex of stem, the antheridia few, without paraphyses, enclosed by several short, ovate, serrulate, costate, brownish leaves: in compact, green tufts, showing the conspicuously white leaf-bases, with branching stems 1–3 cm. high; stem-leaves more or less twisted and crispate when dry, from an obovate or oblanceolate, nearly or quite entire, erect base narrowed to a linear-lanceolate or nearly linear, deeply grooved point from mostly as long to about twice longer than basal part, with a hyaline or yellowish border, entire except at the broadly acute, denticulate apex; costa not quite percurrent, smooth

on both sides except at the denticulate apex, about one sixth the width of leaf at middle, in cross-section showing mostly four guide-cells, a stereid band much larger below than above and outer cells not differentiated; cells of upper part of leaf rather obscure, about 6 μ in diameter, densely papillose on both sides; cancellinae filling most of basal part of leaf, somewhat rounded or truncate above; outer perichaetial leaves much like the stem-leaves, the two or three inner much smaller, of mostly hyaline cells, often slightly serrulate; seta up to 5 or 6 mm. long, not quite smooth above; capsule erect, oblong, scarcely 1.5 mm. long, with convex-conical, rostrate lid about 1 mm. long; peristome-teeth golden-brown, not quite smooth, lanceolate, entire, projecting about 80 μ above the rim of capsule with rather prominent articulations; spores rough, 12–14 μ in diameter; calyptra not seen. [FIG. 7.]

TYPE LOCALITY: Isle of St. Catharine, Brazil.

DISTRIBUTION: West Indies and northern South America.

ILLUSTRATION: Ann. Sci. Nat. II. **2**: *pl. 16, f. 3*.

8. SYRRHOPODON INFLEXUS Mitt. Jour. Linn. Soc. **12**: 117. 1869

Syrrhopodon Sartorii C. Müll. Linnaea **37**: 633. 1874.

Male flowers unknown: in compact, green tufts with somewhat branching stems up to 2 cm. high; stem-leaves with conspicuous, white, imbricate base, twisted and crispate in upper part when dry, up to about 3 mm. long, from an oblanceolate base with entire margin, usually one half to two fifths the length of leaf, gradually narrowed to a nearly linear, grooved point with distinct, entire, pale yellowish border not quite reaching the rather broad, toothed and apiculate apex which sometimes bears numerous spindle-formed or club-shaped propagula up to 100 μ long, with six to eight cross-walls; costa usually smooth except on the more or less spiny-dentate back toward the apex, in cross section showing about five guide cells, stereid bands above and below, the upper band much smaller than the lower and the outer cells not differentiated; cells throughout upper part of leaf mostly rather obscure, highly mamillose or papillose or sometimes almost spiny on both sides, the median about 8 μ in diameter; cancellinae filling most of erect base of leaf, usually rounded above; inner perichaetial leaves much shorter than outer, about 1.5 mm. long, with very short, green, serrulate points; pedicel 4–5 mm. long, bearing an oblong capsule 1–1.5 mm. long with slender-beaked lid about one half as long; peristome-teeth golden-brown, lanceolate, nearly smooth, with rather distinct articulations, projecting above the mouth about 100 μ; spores rough, 14–15 μ in diameter; calyptra rough in upper third. [FIG. 8.]

TYPE LOCALITY: Colombia near Bogota at 6000 ft. alt.
DISTRIBUTION: known only from Mexico and Colombia.

9. SYRRHOPODON HUSNOTI Besch. Ann. Sci. Nat. VI. 3: 195. 1876

Flowers and fruit unknown: in loose, brownish green tufts with slender, fragile, more or less branching stems up to 4 cm. high; stem-leaves from a conspicous, white, imbricate, oblong-linear or oblanceolate, entire base about 1.5 mm. long, somewhat narrowed to an abruptly spreading nearly straight, setaceous, more or less twisted point two and one half to three times longer, with pale yellowish, cylindric border, entire except at the dentate, acute, or somewhat rounded apex; costa not quite percurrent, smooth on both sides except at the denticulate apex, one half up leaf one third to one fourth the width of leaf, in cross-section showing four guide cells, stereid bands above and below with outer cells not differentiated; cells of upper leaf rather obscure, papillose on both sides, the median about 6 μ wide and 8–10 μ long; cancellinae nearly filling leaf-base, terminating in mostly acute angles. [FIG. 9.]

TYPE LOCALITY: Guadeloupe.
DISTRIBUTION: Porto Rico, Guadeloupe and Martinique.

10. SYRRHOPODON FLAVESCENS C. Müll. Syn. 1: 541. 1849

Syrrhopodon parvulus Schimp. C. Müll. Syn. 1: 544. 1849.
Syrrhopodon Schwaneckeanus C. Müll. Bot. Zeit. 13: 763. 1855.
Syrrhopodon scaber Mitt. Jour. Linn. Soc. 12: 119. 1869.
Syrrhopodon calymperidianus Besch. Ann. Sci. Nat. VI. 3: 19. 1876.*
Syrrhopodon subviridis Besch. Ann. Sci. Nat. VI. 3: 196. 1876.
Syrrhopodon scaber var. *breviligulatus* C. Müll. Hedwigia 37: 235. 1898.
Syrrhopodon breviligulatus C. Müll. Gen. Musc. 370. 1901.
Syrrhopodon Dussii Broth. Symb. Ant. 3: 422. 1903.

Dioicous: in compact yellowish brown to pale green cushions with branching stems, mostly 1–2 cm. high, bearing radicles at their base and often at the base of easily separating branches; stem-leaves when dry erect-spreading, flexuous, 5–12 mm. long, with an oblong-linear base 1–1.5 mm. long, rather gradually narrowed to a linear point three to eight times longer and about one

* Type specimens not seen but belonging here according to the description.

third as wide as the base, with cylindric, yellowish or hyaline border extending all round and entire except at the acute or somewhat rounded, dentate apex; costa not quite percurrent, more or less spiny-dentate near apex on both sides, in cross-section showing four to eight guide-cells with stereid bands above and below, the outer cells on upper side and usually two or three outer cells next guide cells on either side below, differentiated; leaf-cells rather obscure, often slightly elongate, about $6 \times 6\ \mu$–$8 \times 10\ \mu$, with thickened, minutely papillose walls on both surfaces; cancellinae ending above in narrowly acute angles or sometimes somewhat obtuse, nearly filling leaf-base; perichaetial leaves scarcely differing from upper stem-leaves; seta slender, erect, red, 5–8 mm. long; capsule oblong-cylindric, scarcely 1.5 mm. long, with rostrate lid about 1 mm. long; peristome teeth lanceolate, yellowish, papillose, projecting above the mouth about 100 μ, with often indistinct articulations; spores minutely roughened, about 12 μ in diameter; calyptra extending two thirds down capsule, somewhat rough at apex. [FIG. 10.]

TYPE LOCALITY: Trinidad.

DISTRIBUTION: throughout the West Indies and northern South America to Mexico.

11. SYRRHOPODON TENUIFOLIUS (Sull.) Mitt. Jour. Linn. Soc. 12: 117. 1869

Calymperes tenuifolius Sull. Proc. Am. Acad. 5: 280. 1861.

Flowers and fruit unknown: in rather loose, pale green to brown tufts with stems mostly under 5 mm. high; stem-leaves from a few millimeters up to over 4 cm. long, from an oblong-linear, entire base about 1.5 mm. long slightly narrowed to a filiform, somewhat grooved point with acute, dentate apex and hyaline or yellowish border of stereid cells entire below the apex; costa not quite percurrent, at apex somewhat rough to spiny-dentate, below on back mostly smooth, on inner side papillose, often to cancellinae, in cross-section showing about six guide-cells with one to three accessory cells on lower side, large stereid bands above and below and outer cells differentiated on upper side only; cells throughout upper part of leaf obscure, mostly angular and slightly elongate, 5–6 μ wide and 6–8 μ long, covered on both sides by more or less compound papillae; cancellinae filling entire base of leaf except a very narrow border above of green cells and terminating above in mostly acute angles. [FIG. 11.]

TYPE LOCALITY: Cuba.

DISTRIBUTION: Cuba, Jamaica and St. Kitts.

None of the specimens examined show propagula, but on the St. Kitts and Jamaican specimens are found young plants, one to three on a leaf, growing from radicles scattered along the leaf point.

12. SYRRHOPODON LYCOPODIOIDES (Sw.) C. Müll. Syn. 1: 538. 1849

Bryum lycopodioides Sw. Prodr. 139. 1788.

Dioicous, male plants more slender than the fertile, bearing several axillary, scattered antheridial buds, the inner perigonial leaves ovate-lanceolate, acute, nearly entire, enclosing numerous antheridia about 0.8 mm. long with few paraphyses: in loose brownish to pale green tufts with somewhat branching stems up to 8–10 cm. high; stem-leaves up to 9 or 10 mm. long, from an oblanceolate, slightly wider, nearly entire, erect base rather gradually narrowed to a spreading, flexuous, linear-lanceolate point with acute apex and bordered all round by a thickened, distantly serrate margin of brown, elongate cells enclosing a small band of stereid cells; costa not quite percurrent, smooth on both sides, about 80 μ wide one half up the leaf and one fifth the width of leaf, in cross-section showing six guide-cells, stereid bands above and below with outer cells differentiated all round; cells of middle and upper blade smooth on both sides, angular, not or slightly elongate, up to 12–14 μ in diameter, in lower leaf and just above the cancellinae often very irregular, transversely or obliquely elongate, with unequally thickened walls; cancellinae mostly broad and somewhat rounded above, filling one half to two thirds the erect leaf-base; perichaetial leaves much like stem-leaves, often longer and extending above the capsule; pedicel about 10 mm. long; capsule ovate-oblong or somewhat spindle-shaped, when dry contracted under the mouth, about 3 mm. long; lid with slender beak about two thirds capsule in length; peristome teeth incurved when dry and not projecting above the mouth, when moist, extending about 80 μ above the rim of capsule, golden brown, very irregular, more or less divided along median line; spores rough, up to 22 μ in diameter; calyptra smooth above. [FIG. 12.]

TYPE LOCALITY: Jamaica.

DISTRIBUTION: Jamaica, Santo Domingo, Guadeloupe, Martinique, Trinidad and northern South America.

ILLUSTRATION: Hedw. Sp. Musc. Suppl. *pl. 40.*

13. SYRRHOPODON RECURVULUS Mitt. Jour. Linn. Soc. 12: 120. 1869

Dioicous, the male plants about like the fertile in habit, with numerous antherieial buds on very short axillary branches or terminal, the outer perigonial leaves about 1 mm. long, the inner one half as long, ovate, acute, costate, serrulate, enclosing about four antheridia without paraphyses: in compact, green mats with conspicuous, white leaf-bases and branching stems 1–2 cm. high; stem-leaves up to 3 mm. long, crispate when dry, from a somewhat oblanceolate or oblong base, ciliate to nearly entire on border, gradually narrowed to a nearly linear or linear-lanceolate point about one and one half times longer, with acute, slightly serrulate apex and pale yellow border entire below the apex, costa nearly percurrent, smooth on both sides except at the dentate or spiny-dentate apex, about 25 μ wide and one sixth width of leaf one half down, in cross-section near middle showing about four guide-cells with stereid bands above and below and outer cells not differentiated; cells throughout upper part of leaf rather distinct, somewhat angular, not or slightly elongate, about 6 μ wide by 6–8 μ long, rather densely papillate and mamillate on both sides of upper leaf, becoming more distinctly mamillate on upper surface just above the cancellinae; cancellinae nearly filling the erect leaf-base, mostly rounded above; perichaetial leaves much like stem-leaves but inner with shorter, green point; pedicel 6–7 mm. long; capsule oblong, about 1.35 mm. long with slender-beaked lid half as long: peristome-teeth golden brown, lanceolate, papillose with rather indistinct articulations, extending about 100 μ above the rim of capsule; spores rough, 12 μ in diameter; calyptra rough above. [FIG. 13.]

TYPE LOCALITY: Cuba.

DISTRIBUTION: known only from Cuba.

EXSICCATI: Wright's Cuban Mosses *47* (as *S. Gaudichaudii*).

Very similar to *S. Gaudichaudii* but more or less ciliate-toothed on upper margin of leaf-base.

14. **Syrrhopodon graminicola** Williams, sp. nov.

Flowers and fruit unknown: in small, dull green tufts with stout, branching, flexuous stems 1–2 cm. high, bearing incurved-imbricate or sometimes spreading flexuous and more or less crispate leaves when dry; upper stem-leaves from an ovate, nearly or quite entire base 0.75–1.4 mm. wide gradually narrowed to an oblong-linear or oblong-lanceolate, acute and apiculate point up to about twice as long, with hyaline border of elongate cells

extending from base to apex, or sometimes nearly or quite disappearing in the upper one fourth of leaf, the border mostly with small, irregular often geminate teeth to near the base; costa percurrent, 50–125 μ wide and about one seventh the width of leaf one half up from base, slightly serrulate on back in upper part and papillose on upper side from near cancellinae half way or more to apex, in cross-section showing about seven guide-cells with stereid bands above and below and outer cells mostly differentiated on upper side; cells throughout upper part of leaf rather indistinct, scarcely elongate, 6–7 μ in diameter, with usually 2–4 minute papillae on either surface; cancellinae broad, not entirely filling the basal part of leaf, terminating above in mostly acute angles; older stem-leaves often with numerous, slender, cylindrical propagula, 200 to 300 μ long, with about twelve cross-walls, growing from cells of blade near either side of costa a little above the cancellinae on the upper surface of leaf and extending half way or more to the apex. [FIG. 14.]

TYPE collected in Jamaica, growing on bamboo joints, Woodstock, Westmoreland Hills, September, 1907, *E. G. Britton 579* (herbarum of the New York Botanical Garden).

DISTRIBUTION: known only from the type locality and Sierra Nipe, Cuba.

This is somewhat like *S. flexifolius* Mitt., but the cells are smaller, more obscure, less elongate, and densely papillose—not smooth or nearly so, as in *S. flexifolius*.

15. SYRRHOPODON ELONGATUS Sull. Proc. Am. Acad. 5: 280. 1861

Evidently dioicous, male flowers not found: in tall, compact, pale green to brown tufts with erect stems up to 12 cm. high, often bearing at the apex two to four short, fruiting branches with spreading-flexuous to somewhat squarrose leaves from a conspicuous, imbricate, whitish base and abundant tomentum on both stems and leaves; leaves of stem and branches, from an oblong base about 2 mm. long, somewhat spiny-dentate above, narrowed to a recurved, grooved, twisted and flexuous or nearly straight point about 3 mm. long, spiny-dentate above and slightly serrulate on the pale, cylindric border below to the enlarged base; costa excurrent into a thorn-point, about 50 μ wide near the middle, smooth on inner face, spiny-dentate about one half down on the back, in cross-section showing four guide-cells, stereid bands above and below, with outer cells not differentiated; cells throughout upper part of leaf distinct, roundish or slightly elongate,

8–9 μ in diameter, highly mamillose on both sides and more or less minutely papillose with three or four papillae to each cell surface; cancellinae nearly filling the erect base, mostly broad and rounded above; inner perichaetial leaves rather smaller than outer, with base yellowish; seta 15–18 mm. long; capsule oblong-cylindric, small-mouthed, about 2.5 mm. long; peristome-teeth projecting above mouth 125 μ, lanceolate, golden brown, rough, with rather indistinct articulations; spores rough, about 16 μ in diameter; lid with beak about 1.5 mm. long; calyptra descending over one half down capsule, rough in upper half. [FIG. 15.]

TYPE LOCALITY: Cuba: *Wright 49*, sterile specimens (fruit described from specimens collected in 1910 near Woodford, Sierra Nipe, Oriente, *J. A. Shafer 3733*.)

DISTRIBUTION: known only from Cuba.

16. SYRRHOPODON TEXANUS Sull. Musci U. S. 103. 1856

Syrrhopodon alabamensis Lesq. & Schimp.; Jaeger, Ber. St. Gall. Nat. Ges. 1877–78: 413. 1879.

Male plants unknown: in pale green to dusky green cushions with simple or slightly branching stems 2–3 cm. high; stem-leaves more or less crispate and tubulose when dry, erect-spreading when moist, the upper about 4 mm. long, linear-lingulate (or above often consisting of little more than the stout, very rough costa if bearing propagula), from a somewhat broader, ovate base, one fourth or more the entire length, with apex obtuse, often spiny-dentate, and border of leaf pale, irregularly dentate to spiny-dentate almost to the insertion of leaf; costa stout, 90–125 μ in diameter below, vanishing just below apex, very rough on back to below the cancellinae, with irregular, low, somewhat forking or spinose papillae; leaves in cross-section showing a terete costa with six or seven guide-cells, thick stereid bands above and below and differentiated outer cells, the leaf-blade mostly mamillose and finely papillose on upper side, papillose on under side, the margin a cylindrical band of minute, stereid cells extending from a little below the apex to near the cancellinae; cells of lamina variable, mostly roundish, obscure, 6–7 μ in diameter in upper leaf to somewhat pellucid and larger below, at least near the cancellinae; cancellinae either acute or somewhat rounded at apex, the cells toward costa broad, often nearly square; perichaetial leaves very similar to upper stem-leaves; seta erect, 1–2 cm. long; capsule ovate-cylindric, contracted at mouth, about 2 mm. long, with slender-beaked lid nearly as long; peristome-teeth short, lanceolate, obtuse, with two or three prominent articulations; calyptra de-

scending to base of capsule, scabrous one third down from apex; spores minutely punctate, about 14 μ in diameter. [FIG. 16.]

TYPE LOCALITY: Texas.

DISTRIBUTION: Texas to Florida and Georgia.

17. SYRRHOPODON LIGULATUS Mont. Syll. 47. 1856

Syrrhopodon crispus Aust. Bot. Gaz. 2: 109. 1877.

Growing in compact, brownish green tufts with mostly simple stems up to 1.5 cm. high; stem-leaves with conspicuously white, imbricate base, crispate above when dry, 2–2.5 mm. long from an obovate-lanceolate base, entire to somewhat serrulate in upper part, slightly narrowed to a lingulate, grooved point, from scarcely as long to about one and one half times longer than the base, with rounded apex and margin crenulate-papillose with short green cells except in lower part, where a narrow, hyaline border of elongate cells is usually present; costa nearly or quite percurrent, slightly serrulate on back toward the apex, smooth below, about one eighth the width of leaf half way up, in cross-section showing toward the base four guide-cells, in upper half mostly two or three guide-cells with stereid bands above and below and no differentiated outer cells, the upper stereid band small, often of only three or four cells; cells of upper blade mostly obscure, not elongate, 6–8 μ in diameter, mamillate and densely papillose on both sides; cancellinae nearly filling the enlarged base, mostly broad and rounded above; perichaetial leaves about like those of the stem; seta 3–4 mm. long; capsule ovate, scarcely 1 mm. long; peristome teeth golden brown, projecting well above the mouth, rather rough, with indistinct articulations; spores rough, 12–15 μ in diameter; lid and calyptra not seen. [FIG. 17.]

TYPE LOCALITY: Guiana.

DISTRIBUTION: Florida, Guadeloupe and Guiana.

18. SYRRHOPODON PARASITICUS (Sw.) Besch. Ann. Sci. Nat. VIII. 1: 298. 1895

Bryum parasiticum Sw. Prodr. 139. 1788.

Encalypta parasitica Sw. Ind. Occ. 1759. 1806.

Calymperes parasiticum Hook. & Grev. in Brewster, Edinb. Jour. Sci. 1: 131. 1824.

Dioicous, the male plants with often two or three rather conspicuous, scattered buds, the inner perigonial leaves very short, broadly ovate-acute, enclosing numerous antheridia about 0.33 mm. long, without paraphyses: plants scattered or in loose tufts

with stems up to 2 cm. high; stem-leaves usually 4–5 mm. long and about 0.65 mm. wide, nearly linear, the basal part often slightly narrower than the upper part, or the terminal leaves at times much shorter and broader, somewhat lanceolate, up to 1 mm. wide, all rather gradually acutely pointed, subtubulose and erect-flexuos when dry, widely spreading, almost squarrose when moist, with a pale, minutely serrulate or entire border of elongate, stereid cells (sometimes quite lacking in the apical leaves) extending from about one third below the apex to four fifths way down the leaf; costa nearly percurrent, smooth on the back except at the slightly denticulate apex, about 60 μ wide near the apex of the cancellinae, in cross-section showing three or four guide-cells, stereid bands above and below them and outer cells not differentiated in the upper part, but more or less differentiated on the ventral side in the lower costa; cells in upper part of blade mamillose on the upper, smooth or unipapillate on the under side, mostly hexagonal and not elongate or slightly so, the median about 8 μ wide by 8–10 μ long, those next the costa on upper side often bearing, from some distance below the apex to near the cancellinae filiform propagulae about 0.5 mm. long, with fifteen to twenty cross-walls; cancellinae filling the most of the leaf-base and terminating in narrow angles next the costa one fourth to one third way up the leaf; perichaetial leaves scarcely differentiated; seta 2–2.5 mm. long, bearing an erect, cylindric capsule about 1.5 mm. long; median exothecal cells more or less four-to-six-sided, 20–25 μ in diameter, with thick walls; peristome and lid not seen; calyptra (immature and not fissured) with rather narrow base, gradually tapering upward and rough throughout. [FIG. 18.]

TYPE LOCALITY: Hispaniola (Hayti).

DISTRIBUTION: Cuba (*E. G. Britton 5040a*; *Brother Leon 3564*), Hayti, Porto Rico (*5197, E. G. Britton*), Trinidad and Yucatan.

ILLUSTRATION: Schwaegr. Suppl. 2^2: *pl. 17*.

Known only from the original collection until obtained in Cuba by Mrs. Britton. The type specimens do not seem to show any propagula, but these bodies readily fall off as the leaves become older. The species is quite closely related to the South American *S. flexifolius* Mitt., which has similar propagula, but the latter has larger leaf-cells and a border extending nearer to both the base and the less acute apex while the cancellinae do not form so narrow an angle upward.

Lindberg* has given a rather full description of this species and

* Öfv. Kongl. Vet. Akad. Forh. **21**: 604–5. 1864.

considers it to be dioicous; he retains it under *Calymperes* although describing a peristome of sixteen teeth that hardly project above the rim of the capsule, a pale, narrow border as in *Syrrholodon* and a calyptra split on one side; a sterile specimen is also mentioned as bearing filiform propagula as in the recent collections; the lid is said to be subulate and as long as the capsule, but both mature lids and calyptras seem to be unknown in any available collection.

19. **Syrrhopodon filigerus** (Aust.) Williams, comb. nov.

Calymperes filigera Aust. Bot. Gaz. 4: 151. 1879.

Flowers and fruit unknown: in thin, dusky green mats with stems 6–8 mm. high; leaves mostly 2.5–3.5 mm. long, incurved or crispate when dry, from a narrowed, more or less oblong, base becoming slightly wider upward to a point about three fourths up leaf, then gradually narrowing to the broadly acute apex, the leaf-blade somewhat keeled and borders flat and entire or nearly so; costa vanishing in apex, 40–50 μ wide about one half up and one tenth the width of the leaf, sometimes bearing numerous filiform propagula from near the middle half way up to apex; costa in cross-section somewhat semiterete, with six or seven guide-cells, stereid bands above and below them and without differentiated outer cells; the cells of leaf-blade mamillose on upper side, finely papillose on under side; border of leaf scarcely extending above the middle, often more or less wanting below, composed of a pale, cylindric band of elongate, stereid cells; cells of blade pellucid, mostly slightly elongate, somewhat angular, the median 7–8 μ wide and 8–10 μ long; cancellinae often extending two fifths up leaf and terminating next the costa in very acute angles. [FIG. 19.]

TYPE LOCALITY: Caloosa, Florida.

DISTRIBUTION: known only from the type locality.

This species is nearly related, by the position of the propagula and shape of leaf, to *S. parasiticus*, but the latter is a larger plant with much wider leaves and costa.

Note.—*S. circinatus* Schimp. is *Symblepharis Schimperianum* (Paris) Card.; *S. crispatus* Hampe is *Didymodon campylocarpus* C. Müll.; *S. fragilis* Hampe is *Trichostomum Schlimii* C. Müll.; *S. strigosus* (Brid.) Mitt., probably does not belong to the Calymperaceae, but the type does not seem to be known in Berlin.

CALYMPERES Sw. (?Weber f. Tab. Calypt. Operc. 1813) in Schwaegr. Suppl. 1²: 333. 1816

Dioicous: plants mostly of medium size, growing in compact tufts with erect, often dichotomous stems, radiculose at the base. Stem-leaves when dry mostly strongly incurved or crispate and subtubulose above the erect, clasping, usually broader and conspicuously white base, the leaf-point varying from lanceolate to lingulate or ligulate with apex often broad. Costa stout, vanishing just below the apex or more or less excurrent, often enlarged and bearing propagula in dense clusters at the apex, from smooth to rough on both sides, sometimes spinose, in cross-section showing from one to three rows of guide-cells with stereid bands above and below and outer cells mostly differentiated. Leaf-margin usually more or less thickened and serrate or sometimes with two serrate wings. Ribbon-like bands of green, elongate cells (teniolae), occasionally wanting, extend just within the margin from base to near apex in some species, in others only for a short distance in the upper basal part of leaf. Cells of upper blade roundish to angular, sometimes shortly elongate, chlorophyllose, often rather obscure, mostly mamillose on upper side and smooth to somewhat mamillose and often papillose on under side; hyaline, rectangular or nearly square cells (cancellinae), usually filling most of basal or sheathing part of leaf, except a narrow border, and changing abruptly into the green cells of blade above (except in *S. fluviatile* which lacks cancellinae). Peristome none. Capsule oblong to cylindric, smooth, on an erect, more or less elongate seta. Calyptra persistent, plicate, rough in upper part, embracing the base of capsule and split on sides only part way down to the base. [PLATE 17.]

Type species: *Calymperes lonchophyllum* Schwaegr.

With cancellinae; teniolae usually present.

Leaf-cells not transversely elongate throughout blade above cancellinae; the spreading blade more or less crispate when dry and not more than 3 or 4 times longer than clasping basal part; guide-cells of costa in one row except in *C. cubense*.

Leaf-margin distinctly serrulate throughout upper part of leaf or entire and basal part somewhat serrulate.

Teniolae extending to or above the middle of leaf.

Green cells of blade mostly up to 7 or 8 μ in diameter and in about forty rows or less from costa to margin in widest part of leaf.

Mamillose cells not terminating in small papillae; teniolae only two or three

cells in from margin in upper basal part of leaf; cancellinae mostly broad and rounded above.

Costa as wide or wider at the base than half way up. 1. *C. Richardi.*

Costa about one half as wide at the base as half way up. 2. *C. cubense.*

Mamillose cells terminating in one or two small papillae; teniolae four to eight cells in from margin in upper basal part.

Cancellinae terminating in acute angles next costa; leaf-base not much broader than blade above. 3. *C. emersum.*

Cancellinae terminating in broad angles or rounded above; leaf-base two or three times wider than blade above. 4. *C. disciforme.*

Green cells of blade about 4 μ in diameter, in fifty to one hundred rows in widest part of leaf; teniolae usually six to twelve cells in from margin in lower leaf and distinct to insertion of leaf. 5. *C. Donnellii.*

Teniolae very short or wanting, only found in upper basal part of leaf when present.

Upper side of costa rough to near cancellinae and teniolae present. 6. *C. nicaraguense.*

Upper side of costa smooth except near apex and teniolae wanting. 7. *C. Heribaudi.*

Leaf-margin entire above and below or slightly serrulate near apex only.

No teniolae; costa rough on both sides to below the middle. 8. *C. Nashii.*

Teniolae short, but usually distinct in upper base; costa smooth, or nearly so, to apex. 9. *C. Guildingii.*

Leaf-cells distinctly transversely elongate except in the small basal part; the spreading leaf-blade nearly straight or somewhat flexuous, rarely somewhat crispate, eight to fifteen times longer than the narrow clasping base; guide-cells of costa in two or three rows.

Leaves up to 15 or 18 mm. long; teniolae mostly more or less evident in basal part; stems under 6 mm. long. 10. *C. lonchophyllum*

Leaves up to 8 or 10 mm. long; teniolae wanting; stems usually much more than 6 mm. high. 11. *C. Levyanum.*

Without cancellinae; teniolae finely developed. 12. *C. fluviatile.*

1. CALYMPERES RICHARDI C. Müll. Syn. 1: 524. 1849

Calymperes Breutelii Besch. Ann. Sci. Nat. VIII. 1: 278. 1895.
Calymperes guadalupense Besch. Ann. Sci. Nat. VIII. 1: 285. 1895.

Calymperes hexagonum Besch. Ann. Sci. Nat. VIII. 1: 286. 1895.
Calymperes Hookeri Besch. Ann. Sci. Nat. VIII. 1: 287. 1895.
Calymperes panamae Besch. Ann. Sci. Nat. VIII. 1: 298. 1985.

In compact cushions with sometimes branching stems 5–6 mm., or rarely up to 2 cm. high; leaves strongly incurved or crispate when dry, the lower short, ovate, about 0.75 mm. wide by 1.5 mm. long, the upper 3–3.5 mm. long, from a variable base, sometimes distinctly ovate or obovate and considerably wider than blade above, sometimes scarcely or not wider than above, and extending into a broadly acute or obtuse point, or those leaves bearing propagulae narrowed above to a stout point without distinct blade and of variable length, with rounded apex; leaf-margin entire except along upper part of clasping base, which is more or less irregularly serrulate; costa stout, vanishing just below apex, rough on both sides above, slightly rough or smooth below the middle and bearing often on upper side at apex a dense cluster of narrowly spindle-shaped propagula, up to 250 μ long with ten to fifteen cross-walls; cells of upper leaf mamillose, distinct, mostly roundish, 6–8 μ in diameter; teniolae two or three cells wide and one to five cells in from lower margin, extending nearly three fourths up leaf and running into the thickened border of upper leaf; cancellinae extending one third to one fourth up leaf, broad, mostly rounded above; perichaetial leaves much like stem-leaves but larger below with cancellinae extending higher up; seta erect, about 3 mm. long; capsule 1.5 mm. long, elongate-oval, smooth, without peristome; lid short-rostrate; calyptra persistent, plicate, rough toward apex, clasping the seta below capsule and split mostly along the middle on one side; spores rough, up to 35 μ in diameter. [FIG. 1.]

TYPE LOCALITY: Guiana.

DISTRIBUTION: Florida, Panama and the West Indies to Brazil.

2. **Calymperes cubense** Williams, sp. nov.

Evidently dioicous: growing in compact tufts with mostly simple stems 6–8 mm. high; stem-leaves up to 3 mm. long, from a white, appressed, more or less obovate or obcuneate base rather gradually or somewhat abruptly narrowed into an oblong-linear to lanceolate, more or less acute point from shorter to about one and one half times longer than the basal part, the margins serrulate nearly all round and the point more or less crispate when dry; costa not quite percurrent, very rough on both sides to near the base, widest, 100 μ or more, about half way up and tapering to a base about one half as wide, in cross-section near the middle

showing about two rows of guide-cells with an indefinite number of smaller accessory cells and stereid cells in one or two rows at the upper and under surface; leaf-cells pale throughout, very mamillose on the upper surface and smooth or papillose on the under side to the cancellinae, the median cells hexagonal to roundish, about 8 μ in diameter; teniolae one to three cells in from the margin, usually extending from the upper part of the base of the leaf to above the middle, and consisting of a double thickness of one or two rows of elongate, often highly mamillose cells; cancellinae mostly broad and more or less rounded above; inner perichaetial leaves rather longer than stem-leaves and with a smaller base, the archegonia and filiform paraphyses numerous; obclavate, eight- to ten-celled propagula sometimes occur in clusters at the apex of the costa. [FIG. 2.]

TYPE collected in the Sierra de Gavilanes, Santa Clara Province, Cuba, August, 1906, *Brothers Leon & Clement 6773* (herbarium of the New York Botanical Garden).

The peculiar cross-section of the leaf of this species is very similar to that of *C. Dozyanum* Mitt. of Java.

3. CALYMPERES EMERSUM C. Müll. Bull. Herb. Boiss. 5: 189. 1897

In broad, lax, dull-green tufts with stems about 1.5 cm. high; stem-leaves about 4 mm. long, mostly incurved, scarcely crispate when dry, from a somewhat wider, or in the lower leaves narrower, oblong or obovate, serrulate base extending into a broad, oblong-linear point, from not much longer than basal part to about twice longer, with rather abruptly acute, serrulate apex and costa vanishing just below apex or when bearing propagulae, excurrent and enlarged into a stout rough point with the propagulae on all sides near apex; costa in middle of leaf about one tenth the width of leaf, rough on both sides in upper half, in cross-section showing four to six guide-cells, stereid bands above and below and outer cells differentiated on both sides; blade of leaf highly mamillose and papillose on upper side, the under side not mamillose but finely papillose; cells throughout spreading leaf-blade distinct, scarcely or not elongate, angular to roundish, 7–8 μ in diameter, with one or sometimes two papillae on each surface; teniolae extending from or near the base to near the abruptly narrowed apex and only one or two cells in from margin in upper leaf, and four to eight cells in from margin at the broadest basal part; cancellinae often extending nearly one half up leaf next costa and terminating in acute angles; "theca hardly emergent, calyptra finely roughened at apex."—*C. Müller*. [FIG. 3.]

TYPE LOCALITY: Guatemala.

DISTRIBUTION: known only from the type locality and Deering Hammock, Cutler, Dade County, Florida, 1916, *J. K. Small.*

4. CALYMPERES DISCIFORME C. Müll. Linnaea **21**: 183. 1848

Calymperes Wulfschlaegelii Lorentz, Moosst. 168. 1864.

In dull or brownish green cushions with somewhat branching stems up to 1.5 cm. high; leaves, when dry, tubulose and crispate above, on lower stem about 2 mm., on upper stem 3.5 mm. long, from a broad, usually obovate, whitish, clasping base narrowed to a broadly lingulate or linear point one and one half to two times longer, with apex broadly acute or in those leaves bearing propagulae, with apex more elongate and narrowed; leaf-margin finely serrulate, nearly to base, thickened above; costa not quite percurrent or somewhat enlarged above and excurrent, rough on both sides to cancellinae or smoothish in lower part, in cross section showing about 6 guide-cells with stereid bands above and below and outer cells differentiated on upper side; leaf-cells above the cancellinae mostly 7 or 8 μ in diameter, slightly or not elongate, mamillose on both sides with more or less distinct papillae on upper blade; teniola extending to above middle of leaf, about 8 cells in from margin in upper basal part of leaf and 2 or 3 cells in from margin of blade above; cancellinae extending one third to two-fifths up leaf, broadly angular, often rounded above; perichaetial leaves about like upper stem-leaves; seta 4 or 5 mm. long; calyptra persistent, striate, very rough above. [FIG. 4.]

TYPE LOCALITY: Surinam.

DISTRIBUTION: Santo Domingo; also in northern South America. The Florida specimens which have been referred to the above belong either to *C. Richardi* or to *Syrrhopodon filigerus.*

5. CALYMPERES DONNELLII Aust. Bot. Gaz. 4: 151. 1879

Calymperes rufescens Besch. Ann. Sci. Nat. VIII. 1: 266. 1895.
Calymperes Brittoniae Besch. Ann. Sci. Nat. VIII. 1: 278. 1895.
Syrrhopodon Smithii Besch. in Paris, Index, ed. 1, 1255. 1898.
Calymperes portoricense Ren. & Card. Bull. Soc. Bot. Belg. **41**[1]: 57. 1904.

In extensive, green mats with stems from 3 mm. to 1 cm. high; leaves incurved or crispate when dry, the lower 2.5–3 mm. long, the upper about 5 mm. long, from a mostly slightly broader, more

or less ovate base one third to one fourth the entire length of leaf extending into an oblong-linear blade with broadly acute apex, or those bearing propagulae usually abruptly narrowed to a rough, stout point of variable length; leaf-margins incurved, doubly and irregularly serrate above, with thickened margin, below minutely serrulate; costa stout, often very rough on inner face above, and on back from apex to near the cancellinae, in cross-section showing about seven guide-cells with large stereid bands above and below and outer cells differentiated on both surfaces; cells throughout upper leaf mamillose and papillose, roundish, mostly 4–5 μ in diameter; teniolae distinct to the insertion of leaf, eight to twelve cells in from marign in broadest part of leaf, extending about one half up leaf and disappearing in the thickened border; cancellinae extending one third to one fourth up leaf, mostly terminating above in acute angles and composed of square to short rectangular cells; perichaetial leaves few, only about one half as long as upper stem-leaves, enclosing numerous, very long paraphyses; seta dark red, erect, 5 mm. long; capsule cylindric, about 2 mm. long; calyptra scabrous above; spores rough, about 18 μ in diameter. [FIG. 5.]

TYPE LOCALITY: Caloosa, Florida.

DISTRIBUTION: Florida (sterile), Cuba, Jamaica (fertile), Porto Rico and northern South America (Mt. Guayrapurina, *Spruce*, in Mitten Herbarium, fertile).

6. CALYMPERES NICARAGUENSE Ren. & Card. Bull. Soc. Bot. Belg. 33^2: 117. 1894

Calymperes Carionis C. Müll. Bull. Herb. Boiss. 5: 189. 1897.

In broad, dusky green cushions with stems 1.5–2.5 cm. high, bearing crowded leaves up to 4.5 mm. long, crispate when dry; stem-leaves from a broadly obovate or obcuneate base with margins mostly serrulate, abruptly narrowed to a nearly linear point two or three times as long, with thickened, slightly serrulate border and serrulate, blunt apex; upper surface of leaf highly mamillose, under surface nearly smooth or somewhat papillose; costa not quite percurrent, often rough on both sides in upper half, mostly smooth below; leaf in cross-section near middle showing a semiterete costa with eight or ten guide-cells, stereid bands above and below, with outer cells differentiated and a leaf-border of a nearly cylindric band of rather small, not stereid cells; cells throughout upper part of leaf rather distinct, somewhat angular or roundish, the median about 6 μ in diameter; teniolae mostly quite distinct, eight or ten cells in from margin, extending

from the lower extremity of the thickened border for only a short distance downward into the basal part of leaf; cancellinae very broad above, mostly terminating in broadly acute angles or somewhat rounded at the apex, scarcely as long as leaf-base; seta erect, 5–6 mm. long; capsule about 2.5 mm. long, cylindric; calyptra persistent, very rough above; spores rough, up to 20 μ in diameter. [FIG. 6.]

TYPE LOCALITY: Nicaragua.

DISTRIBUTION: Nicaragua and Guatemala.

7. CALYMPERES HERIBAUDI Paris & Broth. in E. & P. Nat. Pfl. 1^3: 1189. 1909

In dark green cushions with stems about 1 cm. high; leaves flexuous or crispate when dry, up to 5 mm. long, from an ovate base about 1.5 mm. long with margins finely serrulate in upper half and mostly entire below, narrowed to a point two to three and one half times longer with thickened, somewhat doubly serrulate border extending from basal part to a little below the mostly blunt and serrulate apex; leaf-surface on upper side highly mamillose, on under side nearly smooth below and mostly papillose above; costa vanishing just below apex, smooth below, rough and often bearing propagulae on upper side near apex; cross-sections near middle of leaf show eight or nine guide-cells, stereid bands above and below, with outer cells differentiated, the blade of one layer of cells and a border of a cylindrical band of six to nine cells enclosing one or two stereid cells; cells throughout upper leaf mostly square to roundish, the median 6–7 μ in diameter; teniolae wanting; cancellinae usually extending highest up next costa and terminating in acute angles; fruit unknown. [FIG. 7.]

TYPE LOCALITY: Panama near David.

DISTRIBUTION: known only from the type locality.

This species is much like *C. nicaraguense* but has rather longer leaves, the basal margin more entire and without teniolae; also the thickened border contains a few stereid cells that seem to be wanting in *C. nicaraguense*, and the costa is mostly smooth on upper side.

8. **Calymperes Nashii** Williams, sp. nov.

In very thin, dusky green cushions or somewhat gregarious, with stems only 2 or 3 mm. high; leaves strongly incurved or crispate when dry, about 2.5 mm. long, oblong-linear from a slightly broader or not broader base; leaf entire with a thick,

cylindric border of short-rectangular, green cells extending from a little below the apex to the erect or clasping basal part; costa nearly cylindric, about 65 μ wide one third up from base, papillose on both sides to cancellinae, usually shortly excurrent, slightly enlarged at the apex and bearing numerous, short, spindle-shaped propagula about 120 μ long, with six to eight transverse walls; cross-sections of costa show about four guide-cells, stereid bands above and below of rather large cells, and outer cells differentiated on upper side; leaf-cells of spreading blade mostly not elongate, the median 4–6 μ in diameter, mamillose on upper side, slightly or not mamillose but more or less papillose on under side; teniolae wanting; cancellinae extending about one fourth up leaf, truncate or somewhat rounded above, mostly four to six rows of cells wide on either side of costa and extending about one half way from costa to margin with the small green cells of blade above descending on outer side in a broad band to or near base; fruit unknown. [FIG. 8.]

TYPE collected in Hayti on trees at sea-level near Port Margot, August, 1903, *G. V. Nash 51* (herbarium of the New York Botanical Garden).

DISTRIBUTION: Hayti, Mona Island and Florida (on hammocks, Adams Key, Dade County, March, 1915, *Small & Mosier 5158*).

This species is much like some of the small forms of *C. Richardi* growing in similar situations, but teniolae are entirely wanting, the leaf-border is entire and the cancellinae are narrower.

9. CALYMPERES GUILDINGII Hook. & Grev. in Brewster, Edinb. Jour. Sci. 3: 223. 1824

Syrrhopodon badius Schimp.; Besch. Ann. Sci. Nat. VI. 3: 197. 1876.

Calymperes guadeloupensis Broth. Symb. Ant. 3: 423. 1903.

In large tufts or mats with stems up to 3–4 cm. high; stem-leaves 4–5 mm. long, flexuous or crispate when dry, erect-spreading when moist, from an ovate or obovate, mostly much broader base narrowed to a linear-lanceolate point about three times longer, the upper surface mamillose, the under smooth, with leaf margins entire or nearly so all round and much thickened from apex to the clasping base; costa stout, nearly percurrent, smooth on both sides, often with propagulae on upper side near apex; cross-sections of leaf near middle show a nearly semiterete costa with five or six guide-cells, stereid bands above and below and outer cells differentiated, with a nearly cylindrical leaf-border composed

of three to five stereid cells surrounded by seven or eight larger outer cells; leaf-cells throughout upper blade distinct, slightly elongate, 6–7 μ wide by 8–10 μ long; teniolae usually distinct in upper part of clasping base, four to eight cells in from margin, merging into the elongate cells of border toward base of leaf and upward soon terminating in the thickened leaf-border; cancellinae extending about one fourth up leaf, mostly terminating in acute angles or sometimes rounded or truncate; perichaetial leaves about like stem-leaves but with higher clasping base and green cells extending more or less downward between the cancellinae and costa; seta erect, 4–5 mm. long; capsule 2 mm. long, cylindric, with conical, short-beaked lid; calyptra plicate, scabrous above. [FIG. 9.]

TYPE LOCALITY: St. Vincent, British West Indies.

DISTRIBUTION: St. Kitts, Guadeloupe, St. Vincent, and Porto Rico.

EXSICCATI: Husnot, Pl. des Antilles, *135*, *195*.

10. CALYMPERES LONCHOPHYLLUM Schwaegr. Suppl. 1^2: 333. 1816

Syrrhopodon venezuelanus Mitt. Jour. Linn. Soc. 12: 125. 1869.
Calymperes asperipes Besch. Ann. Sci. Nat. VIII. 1: 277. 1895.

Dioicous, male plants much like the fertile plants, bearing several oblong flowers about 1 mm. long in the axils of the upper leaves, the perigonial leaves one half to three fourths mm. long, more or less ovate, acutely pointed, pale, costate, slightly serrulate above and enclosing five or six antheridia 0.4 mm. long with quite numerous, longer paraphyses: in low mats with tomentose stems mostly 3–5 mm. high, bearing crowded, ligulate, flexuous, rarely crispate leaves up to 15–18 mm. long; stem-leaves from a narrowly oval base with serrulate margins 0.75–1.5 mm. long, extending into a point ten to fifteen times longer, mostly slightly wider above than below, with thickened, doubly serrulate or sometimes nearly entire borders and acute, serrulate apex; costa nearly percurrent, smooth on both sides, without propagula; cross-sections of leaf about one half down show ten or twelve guide-cells in costa with accessory cells in one or two rows, stereid bands above and below, with outer cells differentiated, and leaf-blade often of a double layer of cells extending from costa to the thick, three-sided border; leaf-cells throughout spreading blade transversely elongate, mostly 4–5 μ by 6–8 μ, smooth on both sides; teniolae not extending into narrowed blade, and from distinct to almost or quite wanting in basal part; cancellinae nearly filling the basal

part of leaf, mostly rounded or truncate above; outer perichaetial leaves much like stem-leaves but the base larger and irregularly serrate or incised above, enclosing a few very small inner leaves and numerous paraphyses; seta 10–12mm. long, often bent, slightly rough in upper half; capsule 2 mm. long; lid with beak one half the capsule in length; spores rough, up to 20 μ in diameter. [FIG. 10.]

TYPE LOCALITY: Guiana.

DISTRIBUTION: Martinique, Guadeloupe, Jamaica, Central and northern South America.

ILLUSTRATION: Schwaegr. Suppl. *pl. 98.*

11. CALYMPERES LEVYANUM Besch. Ann. Sci. Nat. VIII. 1: 290. 1895.

In habit somewhat like *C. lonchophyllum*, but stems longer, 1 cm. or more, and leaves shorter, 8–10 mm. long; stem-leaves from an oblong base, serrulate on margins, about 1 mm. long, narrowed into a ligulate-spatulate point six to eight times longer with broad, mostly acute, serrulate apex and thickened border serrulate above, becoming nearly or quite entire below the middle; costa not quite percurrent, smooth on both sides except near apex; leaves in cross-section showing costa with eight or ten guide-cells, an accessory row of four to five cells, stereid bands above and below with differentiated outer cells, and a leaf-blade of one layer of cells, with a cylindric to three-sided border of eight to ten rows of cells; leaf-cells rather obscure in upper leaf, roundish to slightly transversely elongate, mostly 3–4 μ in diameter and from nearly smooth to minutely papillose on both sides teniolae wanting; cancellinae nearly filling the ovate base, of mostly square cells, at apex rounded or sometimes acutely angled; fruit unknown. [FIG. 11.]

TYPE LOCALITY: Nicaragua.

DISTRIBUTION: known only from the type locality and Cuba.

12. **Calymperes fluviatile** Williams sp. nov.

Flowers and fruit unknown: growing in rather stiff, dark green, loose mats; stems simple, 2–3 cm. long, with inconspicuous radicles; in cross-section somewhat triangular, about 250 μ in diameter, showing a distinct central strand and outer walls composed of about three rows of thick-walled cells; leaves when dry subtubulose and incurved or somewhat crispate, when moist widely spreading, oblong-lingulate, entire, 3–3.5 mm. long by a little over 1 mm. wide about half way up the leaf, somewhat

rounded to the scarcely acute apex and with very distinct teniolae of three or four thicknesses of cells and five or six cells wide extending from some little distance above the base to about an equal distance below the apex, with three to six rows of cells between the tenola and margin; costa about 100 μ wide a little above the base, nearly percurrent, in cross-section, showing five or six guide-cells, large stereid bands above and below them and outer cells somewhat differentiated; cells of blade in upper leaf mostly roundish or slightly elongate, mamillose on the ventral, flat on the dorsal side, the median cells 6–7 μ in diameter, gradually changing toward the base to the not very numerous rectangular cells which are more or less colored and never form distinct cancellinae. [FIG. 12.]

TYPE collected in the vicinity of Utuado, Porto Rico, on wet rocks, March, 1915, *E. G. Britton 5206* (herbarium of the New York Botanical Garden).

DISTRIBUTION: known only from type locality and La Juanita, near Las Marias, Porto Rico.

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Explanation of Plates 15-17

PLATE 15

Cross-sections of *Syrrhopodon* made about halfway down the leaf.

FIG. 1. *Syrrhopodon rigidus* Hook. & Grev., from St. Vincent, × 235.
FIG. 2. *Syrrhopodon Bernoullii* C. Müll., from Panama, × 235.
FIG. 3. *Syrrhopodon floridanus* Sull., from Bermuda, × 235.
FIG. 4. *Syrrhopodon incompletus* Schwaegr., from Cuba, × 235.
FIG. 5. *Syrrhopodon Berterianus* (Brid.) C. Müll., from Hayti, × 350.
FIG. 6. *Syrrhopodon martinicensis* Broth., from Guadeloupe, × 235.
FIG. 7. *Syrrhopodon Gaudichaudii* Mont., from Isle of Pines, × 235.
FIG. 8. *Syrrhopodon inflexus* Mitt., from Colombia, × 235.
FIG. 9. *Syrrhopodon Husnoti* Besch., from Martinique, × 235.
FIG. 10. *Syrrhopodon flavescens* C. Müll., from Trinidad, × 235.

PLATE 16

Cross-sections of *Syrrhopodon* made about half way down the leaf.

FIG. 11. *Syrrhopodon tenuifolius* (Sull.) Mitt., from Jamaica, × 235.
FIG. 12. *Syrrhopodon lycopodioides* (Sw.) C. Müll., from Jamaica, × 235.
FIG. 13. *Syrrhopodon recurvulus* Mitt., from Cuba, × 235.
FIG. 14. *Syrrhopodon graminicola* R. S. Williams, from Jamaica, × 350.
FIG. 15. *Syrrhopodon elongatus* Sull., from Cuba, × 235.
FIG. 16. *Syrrhopodon texanus* Sull., from Texas, × 235.
FIG. 17. *Syrrhopodon ligulatus* Mont., from Florida, × 350.
FIG. 18. *Syrrhopodon parasiticus* (Sw.) Besch., from Hayti, × 235.
FIG. 19. *Syrrhopodon filigerus* (Aust.) R. S. Williams, from Florida, × 350.

PLATE 17

Cross-sections of *Calymperes* made about halfway down the leaf.

FIG. 1. *Calymperes Richardi* C. Müll., from Guiana, × 200.
FIG. 2. *Calymperes cubensis* R. S. Williams, from Cuba, × 200.
FIG. 3. *Calymperes emersum* C. Müll., from Guatemala, × 300.
FIG. 4. *Calymperes disciforme* C. Müll., from Surinam, × 200.
FIG. 5. *Calymperes Donnellii* Aust., from Florida, × 300.
FIG. 6. *Calymperes nicaraguense* Ren. & Card., from Nicaragua, × 200.
FIG. 7. *Calymperes Heribaudi* Paris & Broth., from Panama, × 200.
FIG. 8. *Calymperes Nashii* R. S. Williams, from Hayti, × 300.
FIG. 9. *Calymperes Guildingii* Hook. & Grev., from St. Vincent, × 200.
FIG. 10. *Calymperes lonchophyllum* Schwaegr., from Guadeloupe, × 200.
FIG. 11. *Calymperes Levyanum* Besch., from Nicaragua, × 200.
FIG. 12. *Calymperes fluviatile* R. S. Williams, from Porto Rico, × 200.

Contributions to the Mesozoic flora of the Atlantic coastal plain, XIII.—North Carolina*

EDWARD W. BERRY

(WITH TWO TEXT FIGURES)

The Upper Cretaceous deposits of North Carolina were rather fully described in 1912 by Stephenson.† A systematic account of the Upper Cretaceous of the state, its faunas and floras, was planned by the late Wm. Bullock Clark and manuscripts were prepared for the North Carolina Geologic and Econonic Survey, which included an account of the invertebrate faunas by Stephenson, of the vertebrates by Gilmore and of the plants by the present writer. These were transmitted to the State Survey in 1916 for publication and have since been lost. What is known of the fossil flora is contained in a number of short papers published by the writer‡ between 1907 and 1910, and these include nearly everything of interest. It has seemed proper to bring the additional identifications together in the present contribution so that our knowledge of the flora may be complete as regards the present collected material.

The complete flora is arranged botanically in the following pages with brief annotations where such seemed necessary. All of the material comes from what is known as the Black Creek formation.

Thallophyta

ALGITES AMERICANA Berry

Algites americana Berry, Bull. Torrey Club, **38**: 401. 1911; Maryland Geol. Surv. Upper Cretaceous 758. *pl. 50, f. 1.* 1916.

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* The last previous contribution of this series appeared in Bull. Torrey Club **44**: 167–190. *pl. 7.* 1917.

† Stephenson, L. W. North Carolina Geol. and Econ. Surv. **2**: 111–145, 306–314. 1912.

‡ Berry, E. W. Bull. Torrey Club, **34**: 185–206. *pl. 11–16.* 1907; *Ibid.* **35**: 249–260. *pl. 11–16.* 1908; *Ibid.* **37**: 181–200. *pl. 19–24.* 1910; Johns Hopkins Univ. Cir. II. **7**: 79–91. 1907; Am. Jour. Sci. **25**: 382–386. 1908.

This rather indefinite form is rather common at certain circumscribed localities in the upper part of the Black Creek formation in North Carolina and has also been found in the extension of these beds in South Carolina. It occurs also in the Magothy formation of Maryland.

LOCALITIES: Atlantic Coast Line Bridge, Corbits (Old Union) Bridge, and Horrell Landing, Black River, Sampson County.

Pteridophyta

An undeterminable fern from Court House Bluff, Cape Fear River.

Cycadophyta (?)

CYCADINOCARPUS CIRCULARIS Newberry

PODOZAMITES KNOWLTONI Berry

PODOZAMITES LANCEOLATUS (L. & H.) F. Braun

An extended synonymy of this species was published recently in the Maryland Geological Survey volume on the Upper Cretaceous (p. 772. 1916) and need not be repeated in the present connection. The species is wide ranging both geographically and geologically and is undoubtedly composite. The North Carolina material is fragmentary but cannot be differentiated from the forms universally referred to this species.

LOCALITY: Rockfish Creek near Hope Mills, Cumberland County.

Coniferophyta

TUMION CAROLINIANUM Berry

CEPHALOTAXOSPERMUM CAROLINIANUM Berry

PINUS RARITANENISS Berry

CUNNINGHAMITES ELEGANS (Corda) Endlicher

SEQUOIA MINOR Velenovsky

SEQUOIA HETEROPHYLLA Velenovsky

SEQUOIA REICHENBACHI (Geinitz) Heer

ARAUCARIA BLADENSIS Berry

ARAUCARIA JEFFREYI Berry

ARAUCARIA CLARKI Berry

DAMMARA BOREALIS Heer

BRACHYPHYLLUM MACROCARPUM FORMOSUM Berry

ANDROVETTIA CAROLINENSIS Berry

MORICONIA AMERICANA Berry

Angiospermophyta

ARALES

PISTIA NORDENSKIOLDI (Heer) Berry

Chondrophyllum Nordenskioldi Heer, Fl. Foss. Arct. 3^2 114. *pl. 30, f. 4b; 32, f. 11, 12.* 1874.

Pistia Nordenskioldi Berry, Bull. Torrey Club 37: 189. *pl. 21, f. 1–15.* 1910.

This species has been fully described and figured by the writer in the publication cited. It is exceedingly common at certain localities and in some cases the cuticle is preserved. The epidermal cells are small, prevailingly rectangular and thick walled. The stomata are few and scattered, confined to a single surface of the leaf and altogether absent from the broad leaf bases. They are situated in depressions of the surface and have thin elongated guard cells and two accessory cells.

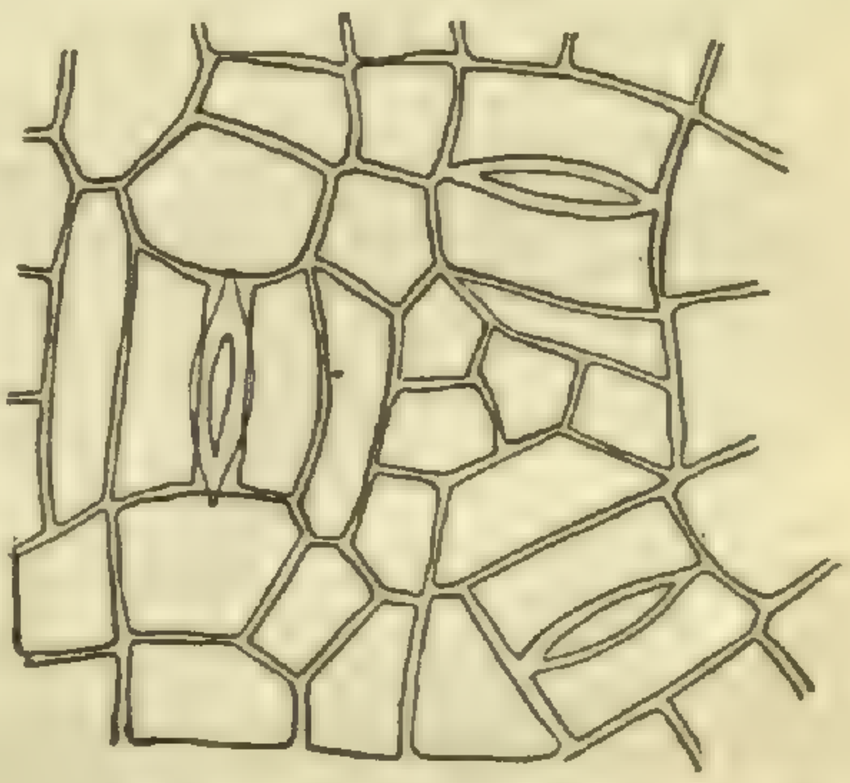

FIG. 1. PISTIA NORDENSKIOLDI (Heer) Berry. Epidermal cell outlines and stomata, × 100.

LOCALITIES: Parker Landing, Tar River, Pitt County; Blackmans Bluff, Neuse River, Wayne County; Sykes Landing (about fifty-seven miles above Wilmington), Corbits Bridge, Big Bend, Atlantic Coast Line Bridge, and Horrell Landing on the Black River, Sampson County.

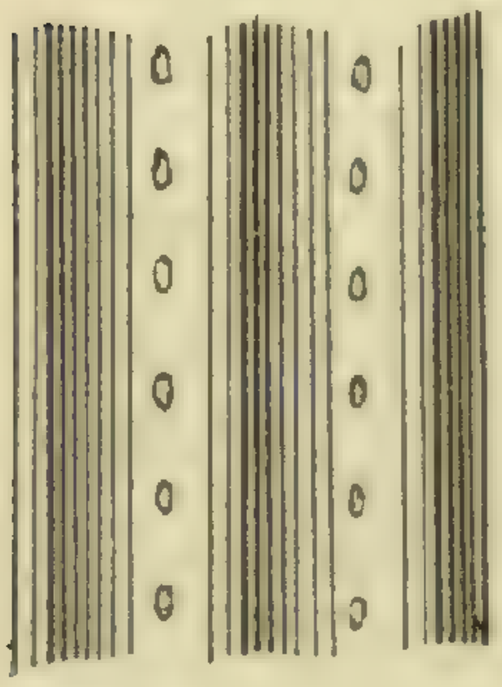

FIG. 2. DORYANTHITES CRETACEA Berry. Longitudinal striations of surface and stomata, × 35.

POALES

PHRAGMITES PRATTI Berry

INCERTAE SEDIS

DORYANTHITES CRETACEA Berry

Doryanthites cretacea Berry, Bull. Torrey Club 38: 406. 1911; U. S. Dept. Int. Geol. Surv. Professional Paper 84: 108. *pl. 17, f. 3.* 1914; *Ibid.* 112: 70. *pl. 13, f. 1.* 1919; Maryland Geol. Surv. Upper Cretaceous 806. *pl. 56, f. 6.* 1916.

This species has been sufficiently described in the papers cited, and it remains to refer briefly to the stomata. The longitudinal

veins are immersed and in the valleys are longitudinal rows of small similarly oriented elliptical stomata with pairs of normal guard cells. Both surfaces of the leaf are exactly alike. This species occurs in the Magothy formation of Maryland, the Eutaw formation of Alabama and Tennessee and the Ripley formation of Georgia and Tennessee. In the Black Creek formation of North Carolina it is found at Rockfish Creek near Hope Mills in Cumberland County and at ninety two and ninety-five and one half miles above Newbern on the Neuse River in Wayne County.

MYRICALES

MYRICA ELEGANS Berry

MYRICA CLIFFWOODENSIS Berry

JUGLANDALES

JUGLANS ARCTICA Heer

SALICALES

SALIX FLEXUOSA Newberry

SALIX NEWBERRYANA Hollick

SALIX LESQUEREUXII Berry

SALIX EUTAWENSIS Berry

FAGALES

QUERCUS? PRATTI Berry

This is an extremely doubtful form of slight botanical interest and is probably not a *Quercus*.

QUERCUS PSEUDOWESTFALICA Berry

Quercus pseudowestfalica Berry, U. S. Dept. Int. Geol. Surv. Professional Paper 84: 35. *pl. 9, f. 5.* 1914.

This species, sufficiently described in the paper cited and based upon material from the Middendorf beds of South Carolina, is found in the Black Creek formation of North Carolina at Court House Bluff, Cape Fear River, Bladen County.

URTICALES

PLANERA CRETACEA Berry

FICUS DAPHNOGENOIDES (Heer) Berry

FICUS INAEQUALIS Lesquereux

FICUS STEPHENSONI Berry
FICUS OVATIFOLIA Berry
FICUS CRASSIPES (Heer) Heer

Proteoides crassipes Heer, Fl. Foss. Arct. **3**[2]: 110. *pl. 31, f. 6–8a.* 1874.

Ficus crassipes Heer, *Ibid.* **6**[2]: 70. *pl. 17, f. 9a; pl. 24, f. 1, 2.* 1882: Lesquereux, Mon. U. S. Geol. Surv. **17**: 79. *pl. 13, f. 3.* 1892; Berry, Bull. Torrey Club **33**: 172. 1906.

The leaves of this species as they occur in the southern Coastal Plain are narrowly lanceolate with a gradually narrowed apex and base, about 15 cm. in length by 2.5 cm. in greatest width, resembling *Ficus atavina* Heer in outline but relatively narrower. The texture is coriaceous and the midrib and petiole often extraordinarily stout. The secondary venation when seen is of the usual camptodrome type with relatively long ascending secondaries. This species was described originally from the Atane beds of western Greenland, the first rather fragmentary specimens collected having suggested the genus Proteoides. It was subsequently recorded from the Dakota sandstone of Kansas. In the Atlantic Coastal Plain it has been found in the Tuscaloosa, Magothy, Eutaw, Middendorf and Ripley formations. In the Black Creek formation of North Carolina it is found at Court House Bluff, Cape Fear River, Bladen County.

FICUS FRUCTUS

Typical *Ficus* fruits occur at several localities in the Black Creek formation. At Court House Bluff they are associated with at least five foliar species of Ficus. They are about 2.3 cm. in length by 1.1 cm. in maximum diameter. Among previously described forms they are very close to, if not identical with, the figs described by Heer from the Atane beds of Greenland and referred on the basis of association to *Ficus atavina* Heer.* The last is a widespread Upper Cretaceous species which has been found in the Middendorf beds of South Carolina.

LOCALITIES: Court House Bluff and Elizabethtown, Cape Fear River, Bladen County.

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* Heer, Fl. Foss. Arct. **3**:[2] 108. *pl. 30, f. 5–7.* 1874.

ARISTOLOCHIALES

Aristolochites Heeri sp. nov.

Leaves of medium or small size, markedly inequilateral in general outline, with a deeply cordate or auriculate inequilateral base and a pointed apex. Margins entire. About 7.5 cm. in length by 4 cm. in maximum width, which is in the basal half of the leaf. Petiole wanting. Midrib stout, prominent, curved. Secondaries stout, diverging from the midrib at wide angles, camptodrome; three or four pairs of reduced caliber diverge fasciculately in the ears from the base of the midrib.

This characteristic species is based upon scanty and fragmentary material. The genus is represented in the Dakota sandstone of the West and in the Arctic Cretaceous, and *Aristolochia*-like fruits and leaves occur from the Eocene onward.

LOCALITY: Court House Bluff, Cape Fear River, Bladen County.

RANALES (?)

DEWALQUEA GROENLANDICA Heer (?)

Dewalquea groenlandica Heer, Fl. Foss. Arct. **6**[2]: 87. *pl. 29, f. 18, 19; pl. 42, f. 5, 6; pl. 44, f. 11.* 1882.

The North Carolina occurrence is based upon incomplete material collected in 1906, and since no additional material has been discovered I have queried the identification. The question of the correctness of this determination is at best of little significance, either geological or biological. There is some question regarding the generic identity between this species and the type of the genus *Dewalquea* which cannot be settled until better material is discovered, and there is also wide difference of opinion regarding the botanical affinities of *Dewalquea*, some students seeing resemblances to the Ranunculaceae and others to the Araliaceae.

LOCALITY: Blackmans Bluff, Neuse River, Wayne County.

CHENOPODIALES

PISONIA CRETACEA Berry

RANALES

MAGNOLIA CAPELLINII Heer

MAGNOLIA NEWBERRYI Berry
LIRIODENDRON DUBIUM Berry
LIRIODENDRON PRIMAEVUM Newberry (?)
MENISPERMITES CYCLOPHYLLUM Lesquereux (?)

Very typical fragments of some species of *Menispermites* are present in the collections. The material is too incomplete for description but indicates a relatively small form very similar to the Dakota sandstone species *Menispermites cyclophyllum* Lesquereux.* The genus is very common in the earlier part of the Upper Cretaceous in both this country and Europe, as well as in the Arctic region, and continues in the Atlantic Coastal Plain well toward the close of the Cretaceous.

LOCALITY: Court House Bluff, Cape Fear River, Bladen County.

ROSALES

LEGUMINOSITES ROBINIAFOLIA Berry
PHASEOLITES FORMUS Lesquereux
GLEDITSIOPHYLLUM TRIACANTHOIDES Berry

GERANIALES

CITROPHYLLUM ALIGERUM (Lesquereux) Berry

Ficus aligera Lesquereux, Fl. Dak. Group 84. *pl. 10, f. 3–6.* 1892.

Citrophyllum aligerum Berry, Bull. Torrey Club **36**: 258. *pl. 18A, f. 1–8.* 1909; Bull. New Jersey Geol. Surv. **3**: 169. *pl. 21, f. 1–8.* 1911; U. S. Dept. Int. Geol. Surv. Professional Paper 84: 47. 1914.

The occurrence of this species in North Carolina is based upon two fragmentary specimens which are in close agreement with the type but with only a slightly and not conspicuously alate petiole. In this last respect it is exactly like some of the material from the Magothy formation.

LOCALITY: Three and a half miles below Dunbar Bridge, Tar River, Edgecomb County.

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* Lesquereux, Cret. & Tert. Flora, 79. *pl. 15, f. 3.* 1883.

EUPHORBIALES

MANIHOTITES GEORGIANA Berry

Manihotites georgiana Berry, Bull. Torrey Club **37**: 507. *f. 1, 2.* 1910; U. S. Dept. Int. Geol. Surv. Professional Paper 84: 114. *f. 2, 3; pl. 22; 23, 24, f. 4, 5.* 1914.

This remarkable species has been fully described in the publications cited. It is found in the Eutaw formation in Georgia and Tennessee, in the Ripley formation of Georgia and Tennessee and in the upper part of the Bingen sand in Arkansas.

LOCALITY: Neuse River, eighty-seven and a half miles above Newbern, Wayne County.

SAPINDALES

CELASTROPHYLLUM CRENATUM Heer

CELASTROPHYLLUM UNDULATUM Newberry

MALVALES

PTEROSPERMITES CAROLINENSIS Berry

PTEROSPERMITES CREDNERAFOLIA Berry

THYMELEALES

CINNAMOMUM HEERII Lesquereux

MALAPOENNA HORRELLENSIS Berry

LAUROPHYLLUM ELEGANS Hollick

SASSAFRAS ACUTILOBUM Lesquereux

Sassafras acutilobum Lesquereux, Cret. Flora, 79. *pl. 14, f. 1, 2.* 1874.

This species is apparently widely distributed and almost as variable as the modern *Sassafras.*

LOCALITY: Court House Bluff, Cape Fear River, Bladen County.

MYRTALES

EUCALYPTUS ATTENUATA Newberry

EUCALYPTUS LINEARIFOLIA Berry

EUCALYPTUS GEINITZI Heer

The foregoing three species are believed to represent *Myrcia* or some similar genus of the Myrtaceae. They are not considered

to represent *Eucalyptus* and should probably be referred to the form-genus *Myrtophhyllum*.

UMBELLALES

CORNOPHYLLUM OBTUSATUM Berry

Cornophyllum obtusatum Berry, U. S. Dept Int. Geol. Surv. Professional Paper 112: 129. *pl. 26, f. 7, 8.* 1919.

This species is sufficiently described in the publication cited and was based upon material from the Tuscaloosa formation of Alabama.

LOCALITY: Court House Bluff, Cape Fear River, Bladen County.

HEDERA PRIMORDIALIS SAPORTA

ERICALES

ANDROMEDA PARLATORII Heer

ANDROMEDA GRANDIFOLIA Berry

ANDROMEDA NOVAECAESAREAE Hollick

KALMIA BRITTONIANA Hollick (?)

PRIMULALES

MYRSINE BOREALIS Heer

MYRSINE GAUDINI (Lesquereux) Berry

EBENALES

DIOSPYROS PRIMAEVA Heer

GENTIANALES

ACERATES AMBOYENSE Berry

INCERTAE SEDIS

Carpolithus carolinensis sp. nov.

A symmetrically ovate, ligneous, biloculate, compressed capsule, pointed at both ends, about 10 mm. in length and 7 mm. in maximum width, midway between the apex and the base.

Of unknown botanical affinity.

LOCALITY: Big Bend, Black River, Sampson County.

Carpolithus bladenensis sp. nov.

A smooth hard nutlet, drupaceous stone or seed, almost perfectly elliptical in outline when viewed from either the front, side or end. Length 11 mm., width 5 mm., thickness 2.3 mm.

Species obviously distinct, based upon a single specimen from the dark clays of the Black River. In form it suggests such modern stones as those of *Cornus florida* or *Nyssa biflora* but the dark polished surface is perfectly symmetrical. Botanical affinity unknown.

LOCALITY: Atlantic Coast Line Bridge, Black River, Sampson County.

The silicious skeleton of tracheids and fibers*

FOREST B. H. BROWN

(WITH FIVE TEXT FIGURES)

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I. INTRODUCTION AND DISCUSSION OF PROBLEM

It is a remarkable fact that when the water-saturated secondary xylem of the stem is allowed to dry, it shrinks considerably in both radial and tangential diameters but only slightly in length. Conversely, when the dry secondary xylem imbibes water it swells mainly in its radial and tangential dimensions but remains nearly constant in length. The swelling and shrinking of the xylem, therefore, takes place mainly at right angles to the axis of growth. Relative stability of length during the imbibition or evaporation of water is a strongly maked physical property of the xylem in either the living or dead tissues of all woody plants; and the bast, in all cases examined by the writer, has been found to exhibit essentially the same properties of swelling and shrinking as the xylem.

The amount of swelling of the xylem of a large number of species has previously been determined by careful measurements without, however, arriving at a satisfactory explanation of the phenomena observed. The details of anatomy of these tissues have not hitherto made it apparent why one dimension should

* Contribution from the Osborn Botanical Laboratory.

vary independently of another. Nothing in the relative size, shape, or arrangement of the cells would bring about a result of this kind.

In a strand of bast, for example, it is difficult to conceive of any change in the dimensions of the tissue as a whole which would not involve a corresponding change in the dimensions of each component fiber, and this statement would apply equally to the xylem. Hence it is apparent that the basis for an explanation of the phenomena of swelling and shrinking in these mechanical tissues must, in its last analysis, lie, not in the structure of the tissue as composed of cells, but in the structure of the membrane as a part of the cell.

During the years 1917–1920, the writer devoted a portion of the time to a study of the minute structure of the thickened membranes which characterize the mechanical tissues of the stem, and in the course of this work the probable explanation of the phenomena just described became apparent. It was found that longitudinal tracts in the secondary thickening of the wall in the fibers and tracheids of the wood and in the fibers of the bast are more highly mineralized than the material of which the rest of the wall is composed. These mineralized tracts or rods, in which silicious material appears always to be present, run longitudinally from one end of the fiber to the other and constitute a skeleton-like structure (see FIG. 3) which, there is every reason to believe, must have a direct effect upon the physical and mechanical properties of the fiber or tracheid in the walls of which it is imbedded. In contrast to the other parts of the wall substance, these silicious rods imbibe little or no water and hence would neither swell nor shrink with such variation in the amount of imbibition water as may take place in the hygroscopic colloidal material in which they are imbedded, as in a matrix. The matrix, on the other hand, absorbs water freely, so that the dry lignified walls, according to Pfeffer,* may take up as much as 51 per cent of their weight in water. Presumably the colloidal material tends to swell equally in its different axes during imbibition; but the mechanics of movement permitted by the silicious skeleton in relation

* Pfeffer, W. The physiology of plants. English translation. Oxford. Vol. 1, p. 209.

to the colloidal matrix is, to all appearance, such as would almost inhibit any tendency of the fiber or tracheid to swell or shrink longitudinally. Since, however, the rods of the skeleton are not generally connected laterally and would therefore be free to move apart or approach more closely to one another, they would allow the matrix in the spaces between to swell or shrink along any of the transverse diameters of the fibers.

These details in the structure of the cell-wall make it clear that the shrinking or swelling of the xylem or bast would not materially change the longitudinal dimensions of these tissues. Hence the fiber-walls of living tissues, as soon as the silicious skeletons are formed, may function in the diffusion and transport of liquid solutions or may swell or shrink in diameter with the increase or decrease of imbibition water, with the fluctuations of turgor in the cells, or with the changes of sap pressure in the conducting elements; at the same time they may offer the undiminished resistance to longitudinal tension or compression necessary for the mechanical support of the stem. Except for decay, the changes which take place with the death of the cell—in the haulms of rye and other grasses after the ripening of the seed or in the xylem of the tree after one or more years—do not materially affect the structural or physical properties of these tissues.

The writer is indebted to Professors A. W. Evans, G. E. Nichols, and other members of the Department of Botany for material and for many valued suggestions and criticisms throughout the investigation; to Professor H. N. Whitford and other members of the School of Forestry for material of *Tecoma* and other woody plants; and to Professors A. J. Hill of the Department of Chemistry and W. E. Ford of the Department of Mineralogy, to whom portions of the work have been submitted for criticism.

II. HISTOLOGICAL ELEMENTS OF TRACHEIDS AND FIBERS

In the course of the investigation the secondary xylem and, in some cases, the bast of approximately five hundred species were examined by the writer, with the result that the structure of the fiber wall in all was found to be essentially the same. Of

the various species examined, the wood fibers of lapachol-forming* species of *Tecoma* seem as favorable as any for the observation of those details with which this paper is chiefly concerned, and all references to this genus have special application to those species in the vessels of which the sulphur-yellow, monoclynic crystals of lapachol are found.

1. MIDDLE LAMELLA AND PRIMARY THICKENING

In an unstained cross-section of the xylem of *Tecoma* mounted in glycerine, it is observed that the middle lamella and primary thickening of the fiber (FIG. 1, *A*) are highly refractive and not

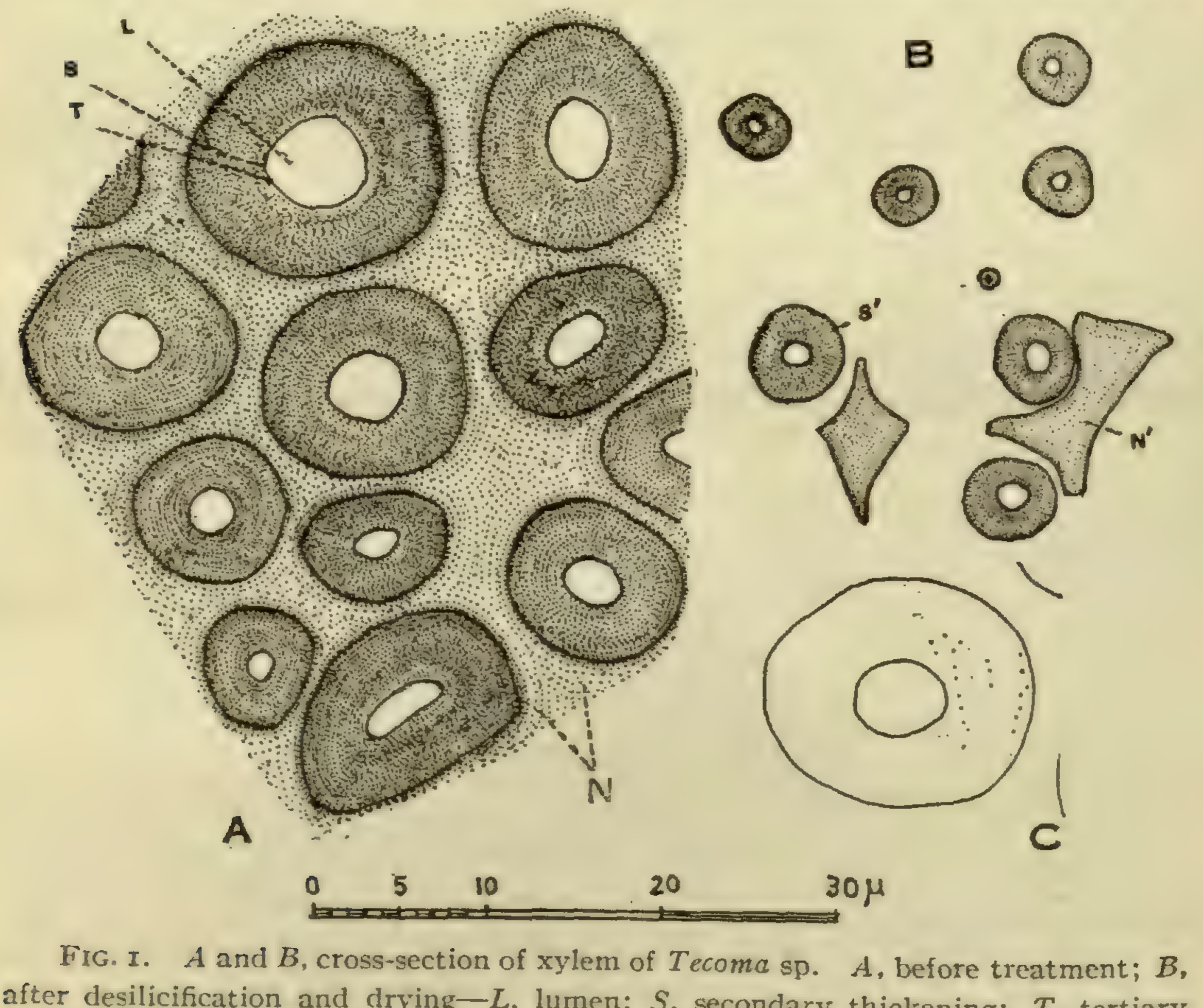

FIG. 1. *A* and *B*, cross-section of xylem of *Tecoma* sp. *A*, before treatment; *B*, after desilicification and drying—*L*, lumen; *S*, secondary thickening; *T*, tertiary thickening; *N*, middle lamella and primary thickening. *C*, secondary thickening of a single tracheid, showing a number of skeleton rods.

* Lapachol is a natural quinone dye, which is found in vessels of the heart-wood of several species of *Tecoma*, natives mainly of South America. It forms a sulphur-yellow dust over the cut surface of the wood and, when moistened by ammonia or dilute sodium carbonate, turns deep wine-red, serving as a reliable character in the identification of the wood. Also, fine chips of the wood, upon standing in a test tube partly filled with dilute aqueous solution of sodium carbonate, will turn the liquid a deepred color.

easily differentiated from each other. In the xylem of *Tecoma* and many other genera, these two membranes differ little from one another in appearance. They stain nearly alike, have nearly the same index of refraction, and are similar in chemical and physical composition, so that, without special technique, they are indistinguishable from one another (as shown in *N*, FIG. 1). They may be differentiated, however, in certain refractive media, as shown by the writer in an earlier paper;* or, better, by mounting cross-sections 10–20 μ thick in dilute Shultze's solution, warming the slide slightly, and observing under high power. In Schultze's solution the true middle lamella is dissovled before the primary thickening of the fiber. These two membranes together compose about one half of the cross-section area, and, when treated with phloroglucinol and hydrochloric acid, give the deep red reaction for furfurol. It is also a noteworthy fact that the index of refraction of these layers, which is about 1.59 (that of the middle lamella being slightly higher than that of the primary thickening), approaches the refractive index of the calcified wall of the calcareous alga *Penicillus* (n = 1.60). *Tecoma* forms an unusually good subject for study because there are few genera in which the primary thickening is as well developed as in this genus. In many genera, even those in which the secondary layer is well developed, as in *Quercus*, *Caesarea*, or *Aspidosperma*, the primary thickening is extremely thin and may even appear to be absent.

2. SECONDARY AND TERTIARY THICKENINGS

The secondary thickening (*S*, FIG. 1) is well developed in all the lapachol-yielding species of *Tecoma*, and appears more or less rounded or even circular in outline in the transverse section. The index of refraction of this thickening of the fiber is slightly below that of quartz, the refractive index of which is 1.54. A thin highly refractive tertiary layer (*T*) borders the lumen (*L*). Neither of these thickenings reacts for furfurol, and both are therefore unlignified in all the lapachol species of *Tecoma* examined. In other genera the thickening is commonly lignified.

When cross-sections are first mounted in glycerine or water, the secondary layer appears to be of homogeneous composition;

* Brown, F. B. H. The refraction of light in plant tissues. Bull. Torrey Club 47: 243–260. *f.* 1–4. 1920.

but, upon standing a few hours, small isolated areas (FIG. 1, *C*) may be distinguished. These areas appear to be slightly more refractive than the material of which the rest of the secondary thickening is composed, when the wall has taken up as much as it will of the liquid in which it is mounted. They are circular in outline, 1–3 μ in diameter, approximately two hundred in number in the cylindrical portion of the fiber, and distributed quite evenly through the secondary thickening of the wall. They are without order of arrangement except that those of larger diameter appear to be placed near the outside. The exact size and position in the fiber wall of areas seen with sufficient clearness to be drawn with the Abbé camera are shown in FIG. 1, *C;* numerous others could be seen distributed evenly through this membrane but not with sufficient clearness to be projected.

One effect of imbibition upon the membrane-mass would be to lower the index of refraction of that portion which takes up the liquid. From the fact that the relatively more refractive areas appear in the membrane after the imbibition of water or glycerine, it is indicated that these portions of the membrane imbibe little or no liquid; the remainder of the membrane, on the other hand, is evidently composed of hygroscopic material. The impermeable areas, in all probability, represent the cut ends of silicious rods which, as will be shown presently, form a skeleton-like structure in the secondary thickening of the fiber.

3. HISTOLOGICAL ELEMENTS OF THE SECONDARY THICKENING

The secondary thickening of fibers of the xylem of *Quercus*, *Hicoria*, *Caesarea*, *Aspidosperma*, and the majority of woody plants forms nearly the entire cell-wall. It is without doubt essential to the mechanical strength of these sclerous membranes and is never absent in fibers the longitudinal dimensions of which tend to remain unchanged under different conditions of moisture.

As previously mentioned, small isolated portions of this thickening of the fiber in *Tecoma* are composed of non-hygroscopic material. If the untreated section is placed upon a mica slip and held over an alcohol flame until the fibers are partly burned to ash, numerous hyaline, non-combustible, rods of mineral composition are left partly free along the burned margin of the secon-

dary layer, held in position by what remains of the charred matrix (FIG. 2, *A*). In all probability the cut ends of these mineralized rods are identical with the small non-hygroscopic areas which were observed in the untreated membrane after being mounted for some time in water or glycerine. The material of which these tracts in the wall are composed is therefore non-hygroscopic as well as non-combustible. The solubility of the rods so isolated was tested in various reagents; but such results can have little significance as to the original composition, since the chemical composition, as well as the refractive properties of the rods, was found to undergo great change during the process of burning. In some cases, the rods became covered with a thin film of black material highly resistant to nitric, sulphuric, hydrochloric and even hydrofluoric acid.

As will be shown presently, these rods are composed, in part at least, of silicious material and form a skeleton-like structure in the secondary thickening of the fiber wall. The remainder of the secondary thickening (in which the rods are imbedded) may be termed the colloidal matrix, for reasons which will be given more fully later.

The histology of the secondary thickening of the fibers or tracheids in the wood and of the fibers of the bast in all species examined by the writer is essentially the same as that observed in the xylem of *Tecoma*. It is composed of the following two structural elements, which differ from each other in their physical and mechanical properties as well as in their chemical composition: namely, (1) a non-hygroscopic silicious skeleton imbedded in (2) a hygroscopic colloidal matrix. With little doubt,

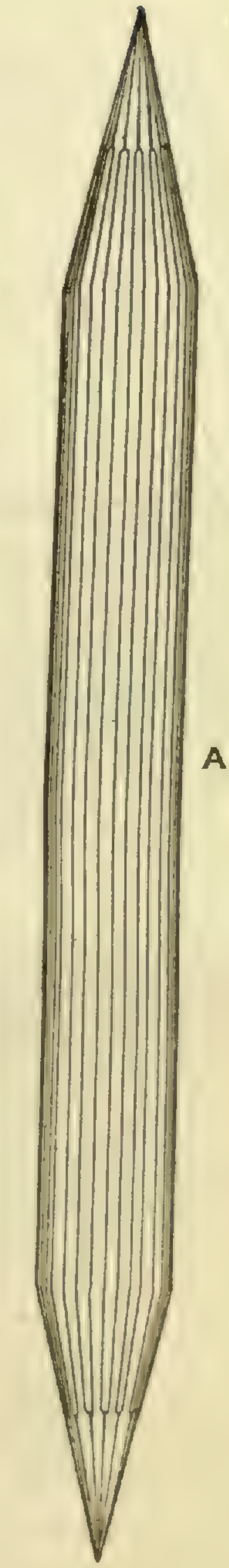

FIG. 2. Silicious skeleton, diagrammatic. *A*. longitudinal view; *B*, transverse view, the shaded portion representing middle lamella and primary thickening.

these structures are independent of each other in the properties which they impart to the wood. They may therefore be separately considered.

a. Silicious skeleton

Structure.—The longitudinal rods, of which the silicious skeleton of tracheids and fibers is composed, are nearly straight, parallel, and extend longitudinally in the colloidal matrix from one end of the tracheid or fiber to the other.

The number of vertical rods in a skeleton varies according to the genus or species, from possibly as few as four in the tracheids of *Trochodendron* to possibly as many as two hundred in the fibers of *Tecoma*.

These rods occasionally branch or coalesce—more frequently in some species than in others. The coalescence probably serves to reduce the number of vertical rods in the tapering ends of a fiber or tracheid, as shown diagrammatically in FIG. 2; in conifers the rods branch around the large circular pits or become reticulate where the pits are numerous; in *Pinus Strobus*, a silicious ring encloses the extreme border of each large pit. Scalariform pitting in particular makes necessary a great reduction in the number of vertical rods in a tracheid. Thus in *Trochodendron* a single rod of comparatively large diameter passes to each side of a vertical series of the transversely elongated pits and a transverse rod of smaller diameter passes between each two pits of the series and joins at either end to each of the vertical rods like the rounds of a ladder. Hence, judging from the structure of the skeleton, the pits and pit-areas would not swell or shrink in either the longitudinal or the transverse planes. The rods are filamentous in shape and are, as before mentioned, probably less than 3 μ in diameter. The details of structure, as summarized above, may be observed in burned preparations, as follows: from small transverse sections of the xylem of *Tecoma* 15–20 μ thick, it is found that as many as twenty rods may be seen partly exposed along the burned outer margin of the secondary layer (FIG. 3, *A*). On burning deeper inward toward the center of the fiber, other rods would undoubtedly be exposed; hence it may be assumed that not less than a hundred rods may be present in the fiber, of which only twenty are exposed at the margin. In unburned

sections mounted in glycerine, the number of rods as estimated from the refractive areas was placed at about two hundred. The difference in estimates from burned and unburned material

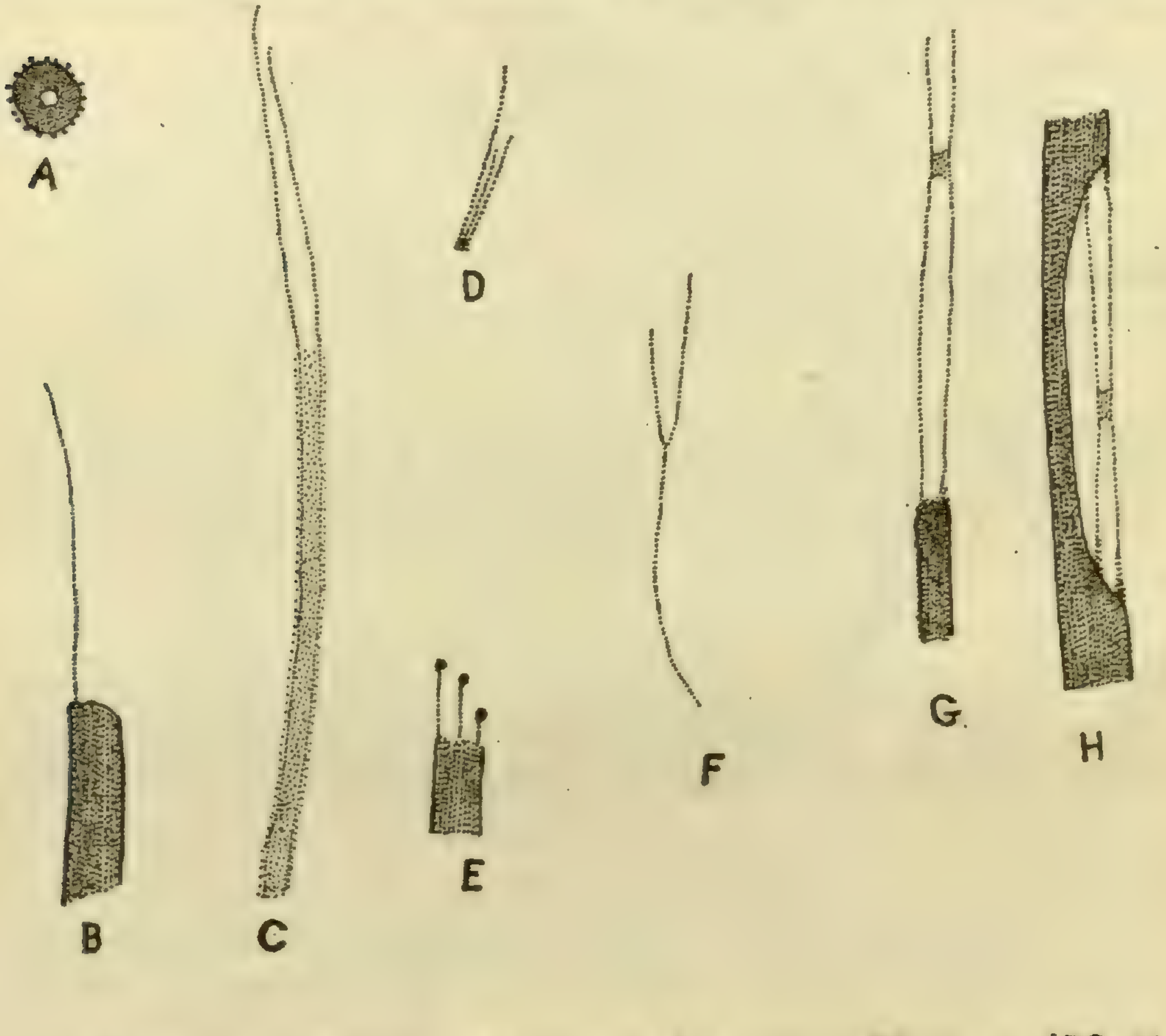

FIG. 3. Burned material. *A*, cross-section of fiber showing exposed skeleton rods; *B*, *C*, *D*, *G*, *H*, showing unbranched rods; *G* and *H*, showing lateral ties; *F*. branched rod; *E*, glass beads formed by heat.

may be explained from the probability that part of the rods in the burned material may have been broken off close to the matrix and therefore were not seen. The number of rods in a fiber of *Tecoma* may therefore be estimated at not less than one hundred and possibly twice that number.

The relative position of the rods in a fiber and the mnaner of branching may be observed from burned macerated material. When the wood of *Tecoma* is treated with Schultze's solution, using 50 per cent nitric acid, it is possible to dissolve away both the middle lamella and primary wall of the fiber. The tertiary

layer in most of the fibers is thin and poorly defined, hence what remains of the fiber wall after thorough maceration is composed almost wholly of secondary thickening. When these macerated fibers are washed, dried, then burned on a mica slip, the isolated or partly isolated rods, and their relative position and branching may be observed. In *B*, FIG. 3, is seen an isolated unbranched rod over 30 μ in length, projecting from the charred end of a partly burned fiber; in *D* are shown three such rods. Two parallel unbranched rods (FIG. 3, *C*) were traced a distance of 90 μ, partly free and partly imbedded in a transparent matrix of unburned material, as shown in the drawing. In burned tracheids of *Trochodendron*, unbranched rods 1.15 mm. in length were found in one instance. Occasionally the rods branch as shown in *F*, from *Tecoma*. The diameter cannot be accurately determined from burned material, since products of combustion and fusion adhere as a film to the outer surface of the rods. It is probable that the lateral ties observed between neighboring rods, as shown in *G* and *H*, FIG. 3, are merely the products of combustion and hence not a structural feature of the skeleton. From such data the structure of the skeleton, as well as its position in the fiber wall, may be inferred. The essential feature of the skeleton consists in the presence of longitudinal rods, and these were never found absent from the fibers and tracheids of the wood or in the fibers of the bast in any species examined by the writer. Other details of the skeleton, however, may vary considerably, according to the species, genus, or family in which it occurs. Thus, in the thin-walled fibers of *Ochroma lagopus*, the rods are few in number; in the thick-walled fibers of *Tecoma*, *Aspidosperma*, *Caesarea*, *Cedrela*, *Swietenia* and *Hicoria*, they are numerous; in *Guaiacum*, they are numerous and of extremely small diameter; in *Pinus Strobus*, they are relatively much branched; in *Araucaria brasiliana*, they are few and of unequal diameter. Silicious rods are present in the fibrous strands in the haulms of *Secale cereale*, but in the walls of the epidermis the silica is distributed more uniformly, so that, after burning, the cellular structure including the guard cells of the stomata is preserved.

Chemical composition.—The skeleton-rods in all species examined were found to be composed, in large part at least, of non-

combustible material. That the chemical composition varies in different species is certain, but silica or some silicate is evidently present in very case. That the skeleton-rods of *Tecoma* are highly silicified is plainly shown from an examination of burned macerated fibers before and after treatment with hydrochloric, nitric, and hydrofluoric acid. Before treatment with acid the rods are invariably present; also, after treatment with hydrochloric or nitric acid they are present; but after treatment with hydrofluoric acid they are invariably absent.

Furthermore, it is of great interest to note that the heat generated by an alcohol flame, together with that of the burning fiber, is sufficient to cause the formation of glass beads, usually at the ends of the silicious rods, as shown in FIG. 3, *E*. This often happens when the calcium-rich fibers of *Tecoma* are burned and less frequently in calcium-poor material like *Secale*. These beads are insoluble in hydrochloric, nitric, or sulphuric acid and have an index of refraction of 1.59, approaching that of flint glass. The calcium is, in all probability, changed to lime by the heat, and would thus act as a flux upon any silica in the rods, causing the formation of the highly refractive glass beads. The result would be the same whether the rods were composed of silica, such as quartz or opal, or of highly silicified material. Also, the same reaction to hydrofluoric acid would be obtained in either case, since either silica or silicates would be quickly dissolved by this reagent.

The question now arises whether the silica in the secondary thickening of the *Tecoma* fiber is actually present in an amount that would be necessary, if it is assumed that the skeleton rods are composed either of silica or of highly silicified material. Macerated material may be used in an approximate anaylsis of the mineral content of this portion of the fiber wall, since in the species of *Tecoma* examined the vessels, ray cells, and elements other than the fibers have thin walls and do not make up a material part of a macerated preparation. It was thus possible to obtain several grams of material made up in large part of the secondary thickening of fibers; after combustion, 1.8 per cent (of the dry weight of the fiber) of mineral matter was obtained and .1 per cent (of the dry weight of the fiber) of silica or silicic acid. Silicon

is therefore not abundant in the secondary thickening of the fiber of *Tecoma*, but if concentrated in the skeleton rods the amount would be more than sufficient to form a skeleton with two hundred vertical rods composed either of silica or of some highly silicified material.

Various evidences make it almost certain that the composition of the rods varies in different families, genera, and species, though silica or silicious matter may always be present. This is indicated in the fact that the effect of hydrofluoric acid upon the mechanical rigidity of the fiber is quite different in some species from what it is in others. Thus in *Tecoma* and several other genera, as will be described more fully presently, the fibrous tissues of the xylem suddenly contract more than 20 per cent in length during treatment with hydrofluoric acid; the wood of *Aspidosperma* and of numerous other genera, on the other hand, is merely softened by this treatment. Also, hydrochloric acid attacks the skeleton rods of *Guaiacum* sp. and softens the wood sufficiently to permisectioning in the microtome; but with this acid there is no material contraction of the fibers, and the skeleton rods are still present in the ash, though a large portion of the outer mineralized film has apparently been dissolved by the acid. In this case the rods may be composed of a central axis of silica or of highly silicified material, enclosed by a thin outer covering of mineral composition which is partly soluble in hydrochloric acid.

That the skeleton rods are not composed entirely of crystalline silica is evident from the fact that when the macerated fibers of *Tecoma*, *Aspidosperma*, *Secale* and all the other genera examined are mounted in strong sulphuric acid, the entire wall is dissolved without leaving any insolubl eremains which might be positively identified as part of a skeleton rod. But the rods seem to be more slowly disintegrated than the matrix, and hence they not infrequently remain visible a short time in the acid after the rest of the wall has been dissolved. The evidences as a whole therefore favor the conclusion that the skeleton rods are composed of highly silicified material, the composition of which varies in the different families, genera, and species.

Physical properties.—As before mentioned, the rods probably imbibe little or no liquid and hence under ordinary temperature

conditions would tend to remain of constant length, though the water content of the matrix might vary considerably. With the application of force, however, the rods would shorten or lengthen within the elastic limits of the material of which they are composed. Under high temperatures the rods appear to undergochange in composition, possibly giving off moisture, and may then be observed to contract in length.

b. Cólloidal matrix

The material in which the skeleton rods are imbedded exhibits essentially the properties of matter in the colloidal state. Besides being highly hygroscopic and gelatin-like in many of its microscopic characters, it has the property of imbibing methylene blue and other colloidal solutions even in the living condition. The term colloidal matrix is therefore used to designate that portion of the secondary thickening of fibers and tracheids in which the silicious skeleton is imbedded; it is apparently stretched upon the silicious skeleton under longitudinal tension strain. This is indicated from the fact that after a macerated fiber of *Tecoma* (*A*, FIG. 4) has remained a few minutes in hydrofluoric acid, it suddenly contracts 36 per cent or more longitudinally, and, at the same time, increases often as much as 100 per cent in diameter, as shown in *B*, FIG. 4,

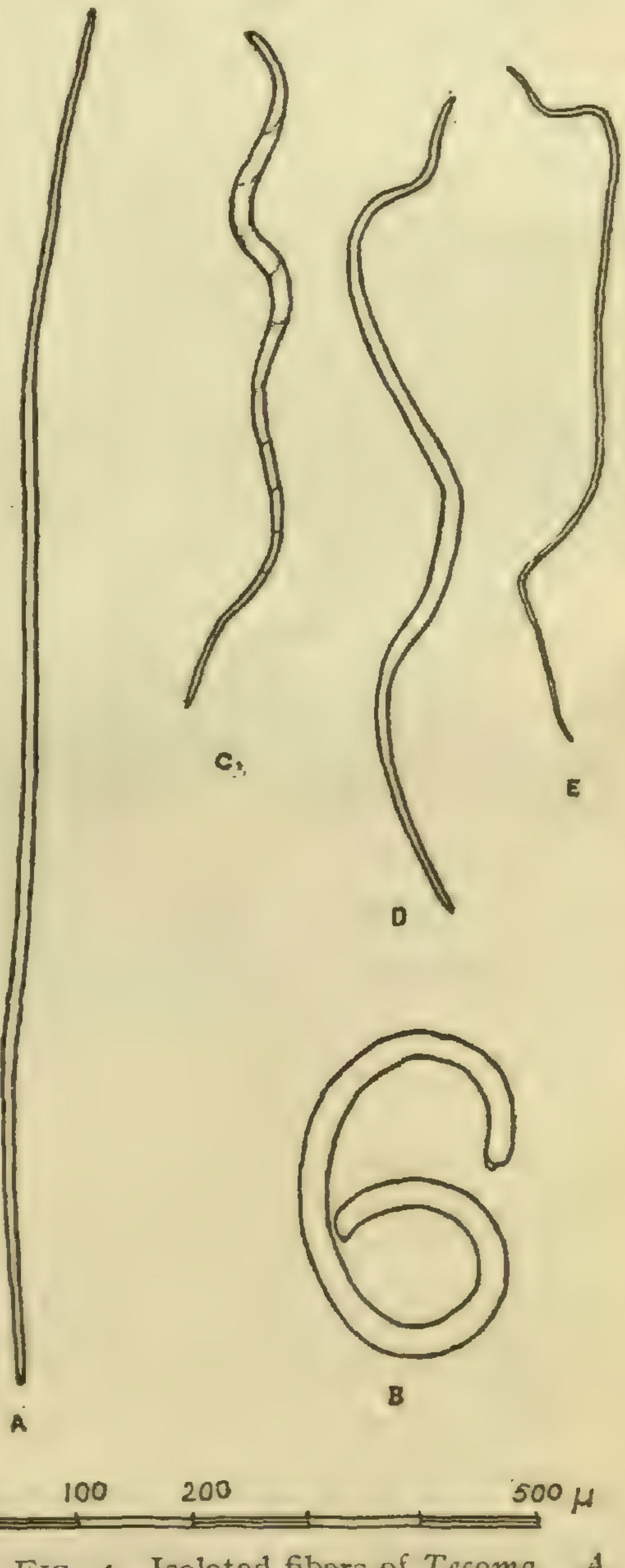

FIG. 4. Isolated fibers of *Tecoma*. *A*, before treatment; *B*, same fiber after desilicification; *C*, *D*, typical desilicified fibers; *C*, showing spirals; *E*, same as *D* after drying.

which is an accurate drawing of *A* after desilicification. Usually the contracting fibers increase much more in diameter toward the center than near the ends, as has been accurately shown in *C* and *D*. In any case the secondary thickening of the fibers contracts in length and expands in diameter with an elastic force sufficient to separate this thickening from the primary thickening, and to burst the mdidle lamella, medullary rays and other parts of the woody tissue sufficiently to allow the transverse expansion.

After the dissolution of the silicious skeleton the colloid matrix is gelatin-like in texture, without mechanical rigidity, and assumes various curved outlines as shown in *B*, *C*, and *D*. It absorbs water freely, and, when dried, shrinks greatly in both diameter and length as shown in *E*, FIG. 4, which is an accurate drawing of *D* after drying. The contraction in diameter is more accurately shown in FIG. 1, *B*, which represents the remains of *A* after desilicification and drying. The primary thickening and middle lamella (*n*) are broken into fragments but shrink comparatively little (*n'*).

The structure of the colloidal matrix may be observed in desilicified fibers mounted in water. Owing to differences in refraction, delicate spiral lines of material may be observed in the body of the matrix as shown in FIG. 4, *C*. Further evidence of the spiral structure of the colloidal matrix is found in the inclination of the slit-like orifices of the fiber pits, which coincides with that of the spirals.

III. INHIBITING EFFECT OF SKELETON UPON THE SWELLING OF THE MATRIX

Since the non-hygroscopic skeleton rods would remain constant in length with the varying moisture content of the matrix, they would inhibit any tendency of the matrix to swell or shrink longitudinally, except in so far as would be permitted by their elasticity. With the application of force, a certain amount of longitudinal compression or stretching of the skeleton rods would undoubtedly be permitted; hence the slight longitudinal swelling and shrinking of woody tissues, which at most amounts to only 1 to 2 per cent, may take place by reason of the elastic property of the rods.

Any tendency of the matrix to shrink or swell along the diameter of the fiber, would not be inhibited by the unbranched vertical rods, since these would move apart or approach with the swelling or shrinking of the matrix. As previously explained, the branching of the skeleton in pit areas would indicate that these areas of the wall swell or shrink only in thickness if at all.

IV. EFFECT OF DESILICIFICATION UPON THE MECHANICAL RIGIDITY OF THE TISSUES

That the silicious skeleton is of fundamental importance to the mechanical rigidity of the tissues is indicated by the effect of desilicification. The haulms of *Secale*, for example, when placed in hydrofluoric acid, contract with elastic force over 30 per cent in length and at the same time expand approximately 100 per cent in diameter. The desilicified tissues have a rubber-like elasticity and may be stretched nearly to the original length.

Remarkably similar effects are obtained when the xylem of *Tecoma* is desilicified. In the accompanying table (TABLE I), the length of a block of wood and the radial and tangential dimension are recorded at indicated intervals during treatment; the gain or loss relative to the respective dimensions of the tissue in the dry state are incased in parentheses.

The rate and relative amount of swelling or contraction in length and in the radial and tangential dimensions of the block, the measurements of which are given in the table during the period of treatment are shown in the graph, FIG. 5. During the five and one half hours in boiling water (*A* to *B*), the tissues swelled barely 1 per cent in length, though both diameters increased more than 10 per cent. At length, all dimensions became stable in water and changed but slightly if at all during the first seventeen hours (*B* to *B'*), when the water-saturated wood was transferred to strong hydrofluoric acid.

Up to time *B'*, only the usual phenomena of swelling in woody tissues are recorded, of which the relative constancy of length is the remarkable but characteristic feature. At *B'*, however, changes of an essentially different character began; the length, which up to this time had remained almost constant, now rapidly contracted over 20 per cent, while the radial and tangential diameters expanded over 40 and over 50 per cent, respectively.

TABLE I

CHANGES IN LENGTH AND DIAMETERS OF XYLEM OF *Tecoma* UNDER DIFFERENT CONDITIONS.

In parentheses is indicated the per cent of gain or loss, relative to dimensions in the dry state.

Length	Radial diameter	Tangential diameter	Hours	Conditions
5.52 mm.	8.53 mm.	8.47 mm.	10.	In air, 100° C.
5.52 "	9.07 " (+6)	9.09 " (+7)	10.5	In water, 100° C.
5.53 " (+0.1)	9.40 " (+10)	9.50 " (+11)	11.0	" " "
5.53 " "	9.48 " (+11)	9.55 " (+12.7)	11.5	" " "
5.53 " "	9.48 " "	9.55 " "	13.0	" " "
5.53 " "	9.48 " "	9.60 " (+13.)	15.0	In HF
5.53 " "	9.48 " "	9.80 " (+15.)	19.0	" "
5.53 " "	9.48 " "	9.80 " "	22.0	" "
5.53 " "	9.48 " "	9.80 " "	32.0	" "
4.7 " (−14.8)	11.3 " (+32)	14.22 " (+67.8)	33.5	" "
4.5 " (−18.0)	12.2 " (+43)	15.7 " (+85)	35.0	" "
4.4 " (−20.3)	11.0 " (+29)	14.5 " (+71)	38.0	" "
4.3 " (−22.0)	11.0 " "	13.3 " (+57)	43.0	" "
4.3 " "	11.0 " "	13.3 " "	48.0	" water
4.3 " "	11.0 " "	13.3 " "	56.0	" "
3.3 " (−40.0)	6.9 " (−19)	7.3 " (−13.8)	56.5	" air, 100° C.
3.3 " "	6.9 " "	7.3 " "	6.4	" " "

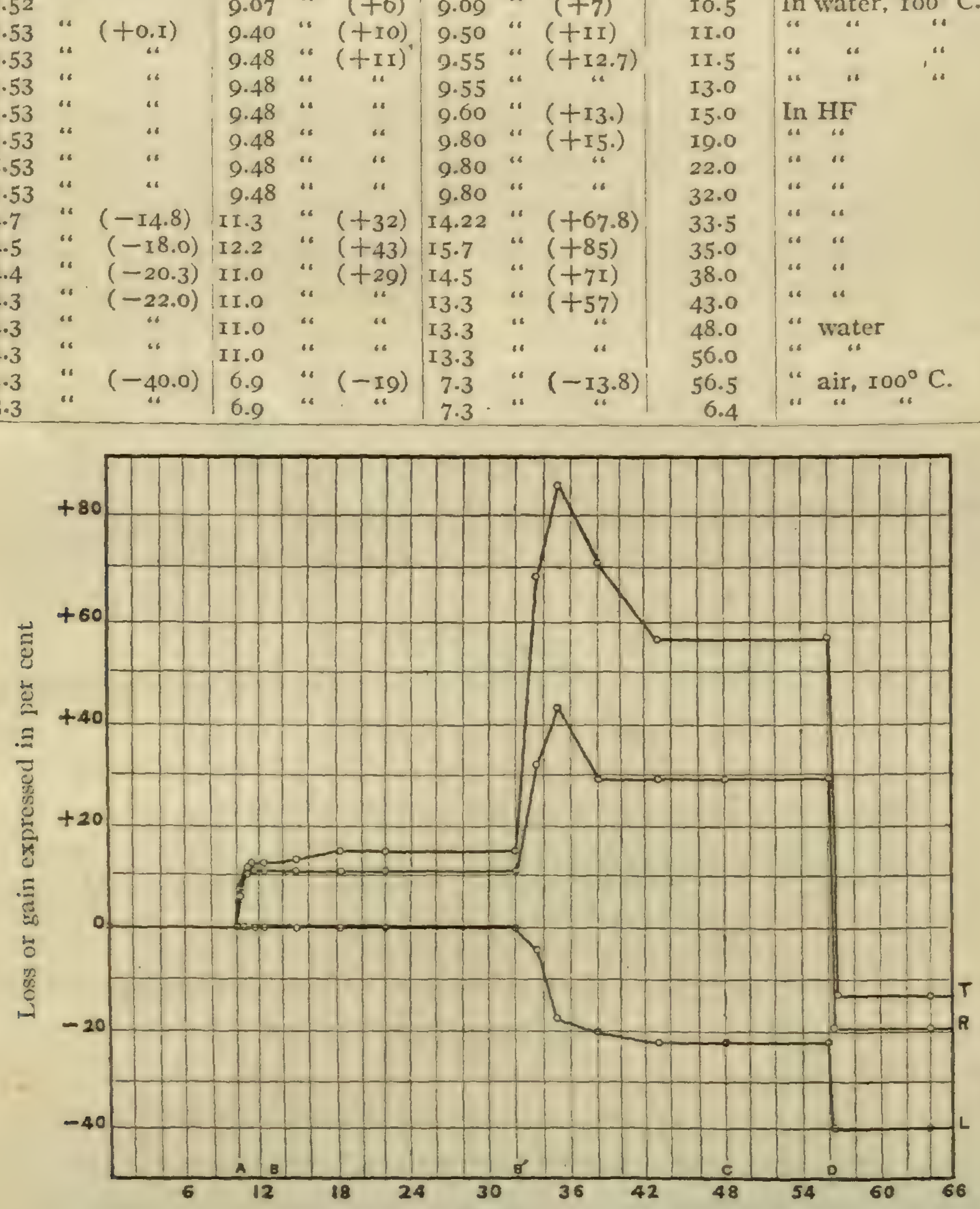

FIG. 5. Graph showing changes in the different dimensions of the xylem of *Tecoma* during treatment; *A*—*B*, in boiling water; *B*—*C*, in hydrofluoric acid. A collapse of mechanical rigidity commences at time, *B′*, *C*—D. in running water; *D*, in air, 100° C.

The transverse dimensions subsequently contracted to some extent, but after a few hours all dimensions remained nearly constant, whether left in acid, or transferred to water (*C* to *D*). The subsequent great contraction (*D*) of all dimensions which took place when the desilicified tissues were dried, indicates the almost complete loss of mechanical rigidity of the xylem after desilicification.

The changes which occur in the longitudinal dimensions of a block of the xylem of *Tecoma* during treatment are essentially the same as those which occur in the isolated fiber under the same treatment. Probably up to time *B'* the skeleton rods had not been weakened by the acid. But immediately after *B'* there was a rapid contraction in length and expansion in the transverse dimensions, such as would occur with the collapse of the skeletons; the entire course of the curves during the first part of the time, *B' C*, indicate the collapse of the mechanical element of the xylem.

A similar amount of longitudinal contraction and transverse expansion occurred in the xylem of all of the thirty lapachol-yielding samples of *Tecoma* examined. Similar changes were observed in approximately one-fifth of the species of the other genera and families examined by the writer; but the amount varied with the genus and species. Many species such as *Aspidosperma*s, showed little or no longitudinal contraction during desilicification. Such differences in the effect of desilicification are reasonably explained on the assumption that the rods must differ in chemical composition, according to the species, although silicious material may be present in each case.

V. SUMMARY

The longitudinal dimensions of the xylem and bast in either living or dead tissues are subject to little variation upon soaking in water or drying, by reason of a silicious skeleton in the secondary thickening of the fibers and tracheids. This skeleton is composed of sparingly branched non-hygroscopic rods of silicified material which extend longitudinally in the hygroscopic cell-membrane from one end of the fiber or tracheid to the other

Except for local areas, the longitudinal skeleton rods are not branched or united in a way to prevent them from being spread

apart or crowded together; hence the swelling and shrinking of the cell-wall may take place at right angles to the axis of growth.

In the vicinity of pits, such as the circular pits of *Pinus Strobus* or the scalariform pits of *Trachodendron*, the vertical system of rods is replaced by reticulate branches or transverse connections which would probably inhibit swelling or shrinking of these areas in all directions except, possibly, in thickness.

The skeleton rods are composed of highly mineralized material, the composition of which varies in the different families, genera, and species; but silica or some silicate is present in at least a large number of cases.

The effect of zinc sulphate on protoplasmic streaming

HESTER M. RUSK

(WITH TWO TEXT FIGURES)

In view of the fact that metallic poisons in minimal doses stimulate the metabolic activity of many plants, as has been shown by the researches of many workers, it seemed a matter of interest to determine whether any ocular evidence of excitation could be observed in individual cells. Of all the poisons employed we have the most data regarding the effect of zinc sulphate, and in this work the observations were limited almost entirely to the action of that salt. A few observations were made with other substances, such as cobalt nitrate and sulphuric acid, but without very definite results. The most convenient visible reaction to observe is the effect on the rotation of protoplasm in active cells. For this purpose cells of the leaf of *Elodea canadensis* and cells from an uncorticated *Chara* were taken.

While the literature is rich regarding the action of metallic poisons on the stimulation of growth and certain of the metabolic processes concerned in the use of nutrient material, there is not a large amount on the effect of irritant substances on the rate of streaming. Ewart (1, p. 87) says, "all concentrations [of metallic poisons] sufficient to produce any effect cause from the outset progressive retardation." He cites only experiments with sodium chloride (0.1–0.5 per cent) and cupric sulphate (0.5–10 per cent), however.

With regard to the effect of metallic poisons on other functions of plants it has been found (1) That zinc sulphate in concentrations from 0.000125 *N* to 0.002 *N* stimulates the growth of *Aspergillus niger* and *Penicillium glaucum*, resulting in an increase of dry weight. The greatest stimulation was obtained by a concentration of from 0.000125 *N* to 0.0005 *N* (see Richards, 2). (2). That the same concentrations of zinc sulphate stimulate the same fungi, causing them to make a more economical use of sugar. The greatest stimulation was obtained by 0.00025 *N* (see Richards, 3). (3) That zinc sulphate in concentrations from

0.0003 *N* to 0.0015 *N* stimulates *Sterigmatocystis nigra* with the result that less nitrogen is fixed by the fungus. The greatest stimulation was obtained by solutions from 0.0003 *N* to 0.001 *N* (see Latham, 4).

For the test solutions in this work Merck's reagent zinc sulphate was used and was kept sealed with paraffin when not in use. It was weighed out on a delicate Becker balance, and a 0.1 *N* stock solution made. For most of the work with *Elodea*, the stock solution was made up in distilled water; but for part of this work, and for all of that with *Chara*, double distilled water was used. Dilutions were made from this stock solution as needed. For all measurements accurately graduated flasks and pipettes were used. Filtered tap water was considered to be a better medium for controls than distilled water, since it is much more like the medium in which these plants naturally live. Hence tap water, filtered through a Berkefeld filter, was used for controls; it was also used for making dilutions from the stock solution of sinc zulphate, so as to make the test solutions differ from the control only in the presence of the zinc sulphate.

A stock supply of the plants was kept in the greenhouse in jars with snails. Small amounts were brought into the laboratory from time to time, and kept in filtered water. Specimens put into test solutions were taken directly from filtered water. The temperature of the water or solution was between 19° and 25° C. at the beginning of all the observations; at the beginning of all but a very few it was between 21° and 24° C. The light used for all the observations was that of a 60-watt lamp coming to the mirror of the microscope through an ammonia copper sulphate globe.

For most of the work with *Elodea* the following method was used: Several healthy looking leaves were taken from the same region of the same stem, and placed, some in a separate dish of filtered water, and some in a similar dish containing about an equal amount of the zinc sulphate solution. One of the leaves from the zinc sulphate solution was then mounted on a slide in some of the same solution, and observations were made on from three to five of its cells. This was done within an hour and a half of the time of starting. Then a leaf from the dish of filtered

water was mounted and observed similarly. This whole proceeding was carried on within two hours and a half.

For the last part of the work with *Elodea*, the method was changed in the following way: The control observations were made first. Then the same leaf was put into the zinc sulphate solution and observed again. It was impossible, however, to test the same cells again. The whole observation was made within an hour and a half; and the specimens were left in the zinc sulphate solution not more than an hour.

The time required for a chloroplast to be carried the length of the cell was determined with a stop-watch that could be read to tenths of a second. Five such observatons were made for each cell and averaged. The length of the cell was then measured with a micrometer eyepiece. From twelve to twenty-five cells were tested for each concentration used. The lengths of the cells timed in one concentration were averaged; the average timings for the cells timed in one concentration were averaged; and the results were reduced so as to express the rate of movement for the concentration in terms of seconds per 100 microns. The results are also expressed in terms of per cent acceleration or retardation of the normal, or control, rate.

Most of the zinc sulphate test observations were made on different leaves from the controls, and all were made on different cells from the controls. On this account, a general average of all the normal observations was considered the best control to use for all concentrations. This base normal rate was an average of the timings of 137 cells.

For all the work with *Chara* the following method was used: A healthy-looking piece was taken from the tip of a plant, and observations were made on from one to four of its cells. The piece was then put into the test solution, and new observations were made on the same cells. Ten normal and ten test observations were made for each cell. All the observations on one piece were made within an hour and a half; and, for the most part, one piece was left in the test solution not longer than three quarters of an hour.

The time required for a particle in the cytoplasm to be carried the whole length of the micrometer scale was determined; under the

magnification used this was a distance of 595 microns. (For one concentration a distance of 420 microns was used.) From fifteen to eighteen cells were tested for each concentration. For the sake of comparison the averages were reduced to seconds per 100 microns, and as for *Elodea*, results are also given in terms of per cent acceleration of the normal.

Since the test and control observations were made on the same cells in every case, no base normal rate was calculated; the average of the normal timings of the particular cells tested for each concentration, was used as the normal for that concentration.

The work with *Chara* was more satisfactory than that with *Elodea* in several ways. Because of the larger size of the cells, it was possible to time the movement through a much greater distance, thus lessening the magnitnde of error. It was possible to obtain the normal rate for the same cells that were tested, thus limiting the factor of individual variation. Because of the greater ease of making observations and of finding suitable cells, it was possible, with the same expenditure of time, to make twice as many observations on each cell, thus again lessening the magnitude of error.

To prevent the crushing of *Chara* cells, the cover-glass was supported on two narrow strips of glass, cut from an ordinary slide. In general, in all this work, observations were made immediately upon placing the material under the microscope, and immediately after placing the material in test solutions. However, in case a cell showed a steady rise or fall in its rate, observations were continued until the rate became fairly uniform for the five or ten necessary consecutive observations. Uniformity was usually reached in a few minutes.

By reference to TABLE I and FIG. 1, it will be seen that very weak zinc sulphate solutions, 0.0002 *N* to 0.001 *N*, do accelerate the movement in *Elodea* cells. The concentration at which the greatest acceleration was observed was 0.0003 *N*, the acceleration being 14.85 per cent of the normal rate. Acceleration becomes less blow this concentration, and also falls off as the concentration rises. At 0.0015 *N* retardation is seen. There appears to be some irregularity in the retardation, but that was not the phenomenon of special interest in this study. By reference to TABLE II and

TABLE I

ELODEA

Fraction N $ZnSO_4$	No. of cells tested	Average distance in microns	Rate per 100 microns in seconds	% Acceleration of normal	% Retardation of normal
0.0000	137	105.30	16.83	0	0
0.0002	23	96.80	14.66	12.88	
0.0003	25	104.50	14.33	14.85	
0.0005	12	136.15	15.75	6.42	
0.0010	12	99.05	16.45	2.26	
0.0015	14	105.90	18.12		7.66
0.0020	19	120.50	17.26		2.56

FIG. 2 it will be seen that very weak zinc sulphate solutions, 0.0004 *N* to 0.0015 *N*, do accelerate the movement in *Chara* cells. The concentration at which the greatest acceleration was observed is 0.001 *N*, the acceleration being 20.58 per cent of the normal

FIG. 1. Graph showing per cent acceleration (above "Normal" line) and retardation (below "Normal" line) of movement in *Elodea* cells by solutions of zinc sulphate.

rate. Acceleration becomes less below this strength until at 0.0003 *N* there is no effect at all. Acceleration also falls off as the strength increases, until at 0.002 *N* there is no effect. Higher concentrations were not investigated.

TABLE II

CHARA

Fraction N $ZnSO_4$		No. of cells tested	Distance in microns	Rate per 100 microns in seconds	% Acceleration of normal
1	0.0000	18	595	2.485	0
	0.0003	18	595	2.485	0
2	0.0000	18	595	2.92	0
	0.0004	18	595	2.82	3.4
3	0.0000	18	595	2.69	0
	0.0005	18	595	2.41	10.41
4	0.0000	15	420	4.18	0
	0.0010	15	420	3.32	20.58
5	0.0000	18	595	2.71	0
	0.0015	18	595	2.45	9.6
6	0.0000	18	595	2.45	0
	0.0020	18	595	2.45	0

It appears, then, that *Elodea* cells are sensitive to weaker zinc sulphate than *Chara* cells, but that the maximum acceleration is less. It is also evident that the concentrations of zinc sulphate found by this study to cause the greatest acceleration of streaming

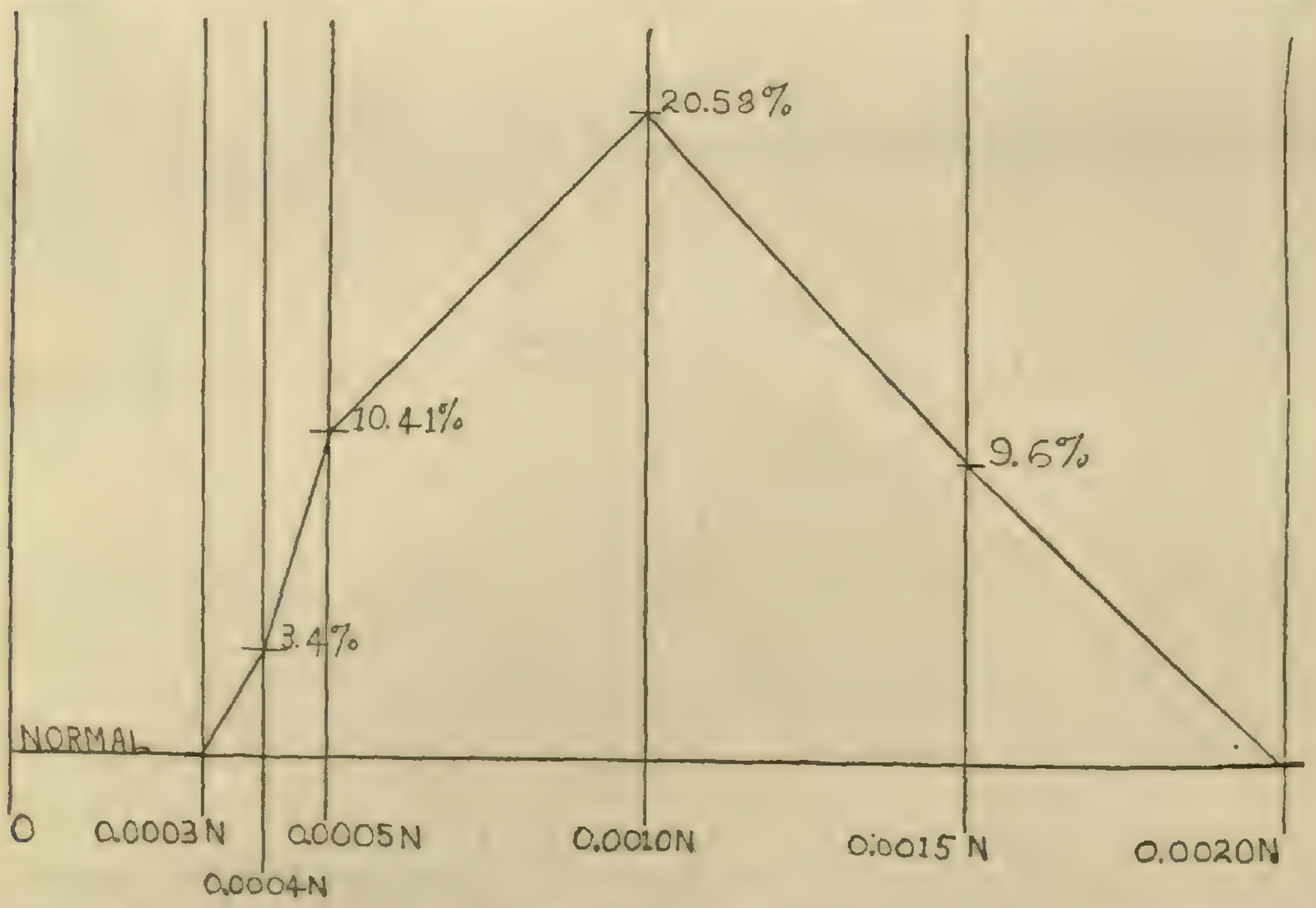

FIG. 2. Graph showing per cent acceleration of movement in *Chara* cells by solutions of zinc sulphate.

in *Elodea* and *Chara*, are in the neighborhood of those found to cause the greatest stimulation of the growth and metabolic activities in certain fungi by the work of Richards (2, 3) and Latham (4) already referred to.

The results of this study are offered as additional evidence that very dilute poisons act as stimulants to plant cells.

This work was done at the suggestion and under the direction of Dr. Herbert M. Richards, to whom the writer is greatly indebted for advice and encouragement.

BOTANICAL LABORATORY,
BARNARD COLLEGE,
COLUMBIA UNIVERSITY.

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INDEX TO AMERICAN BOTANICAL LITERATURE

1914–1920

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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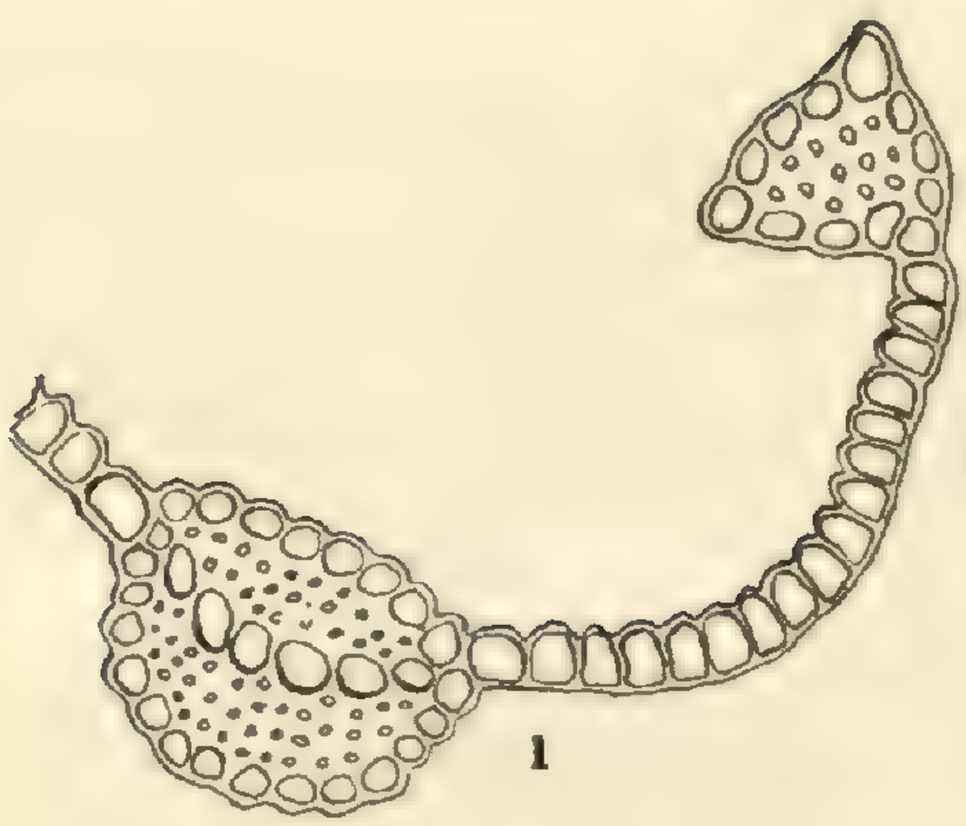

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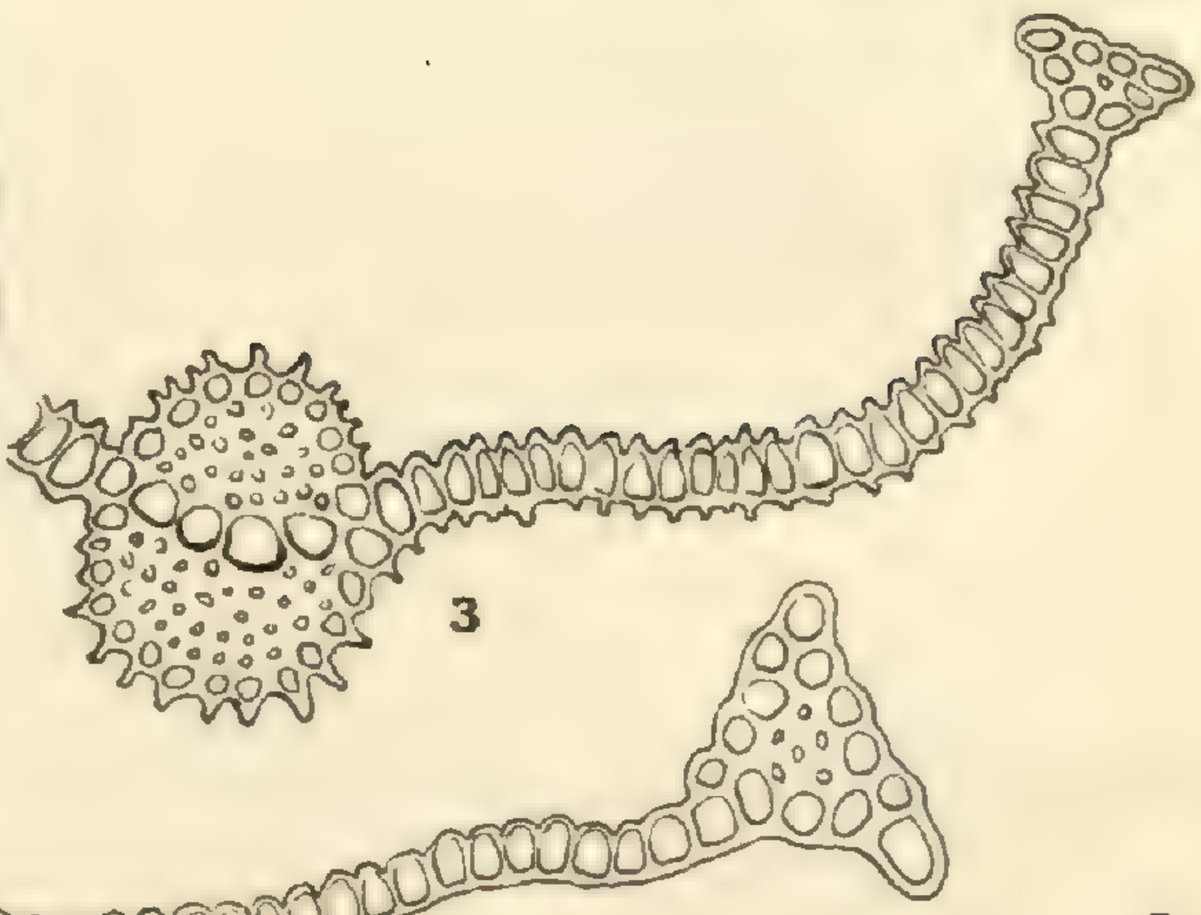

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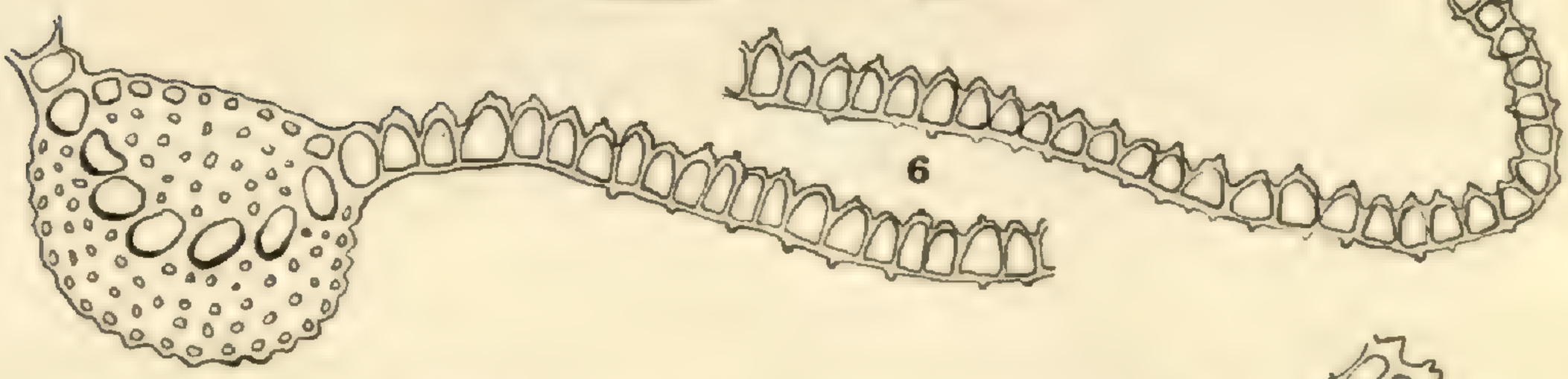

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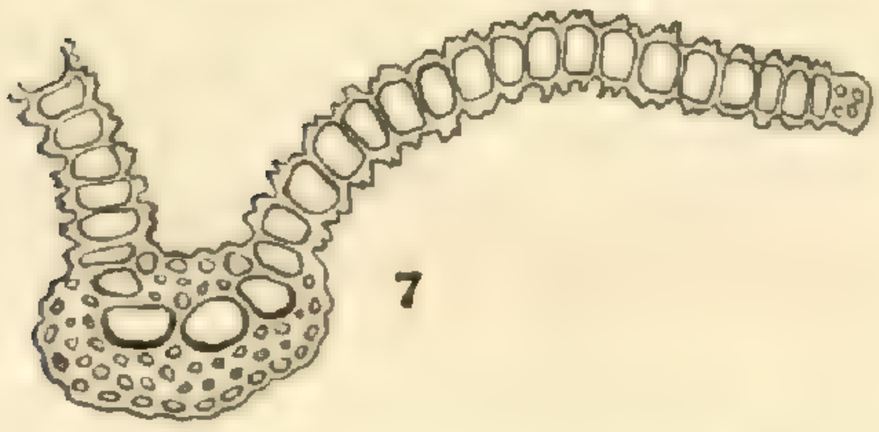

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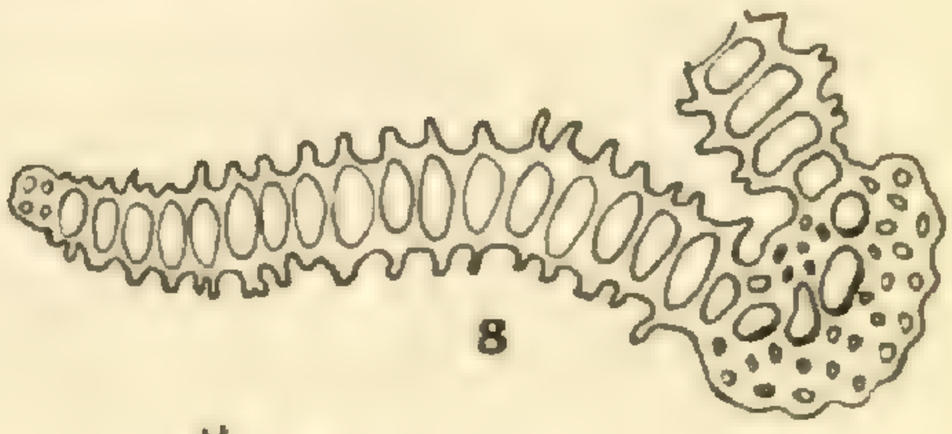

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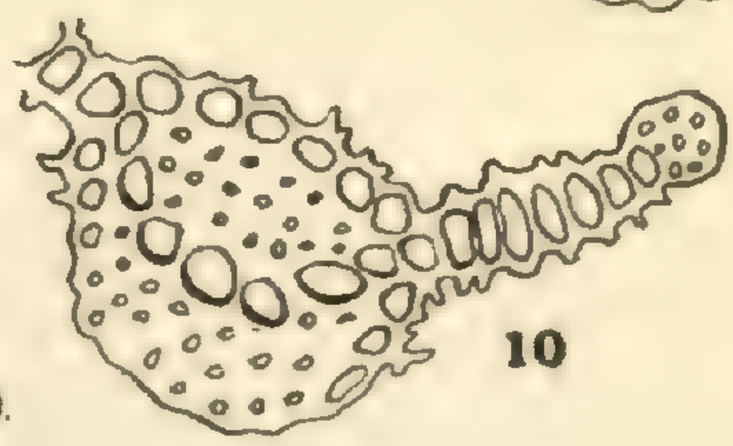

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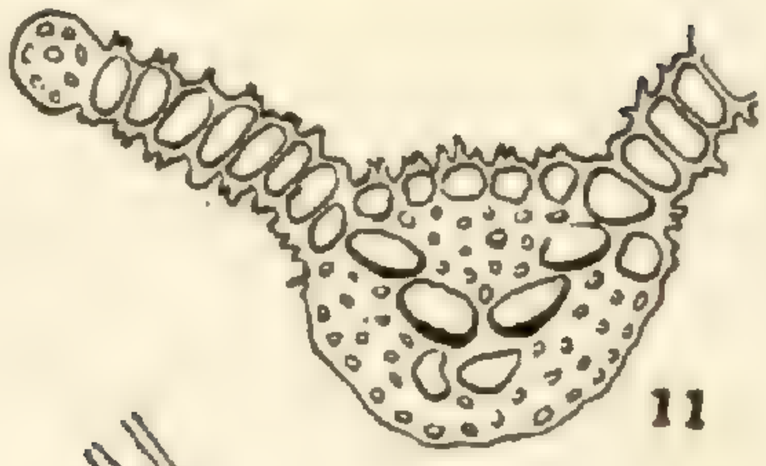

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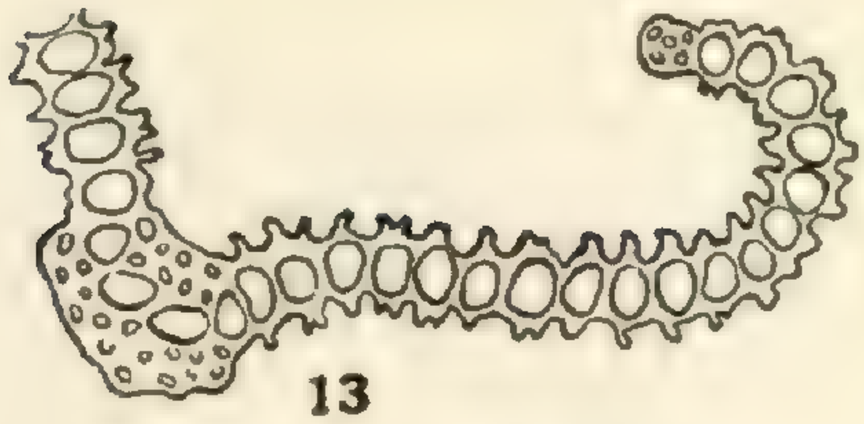

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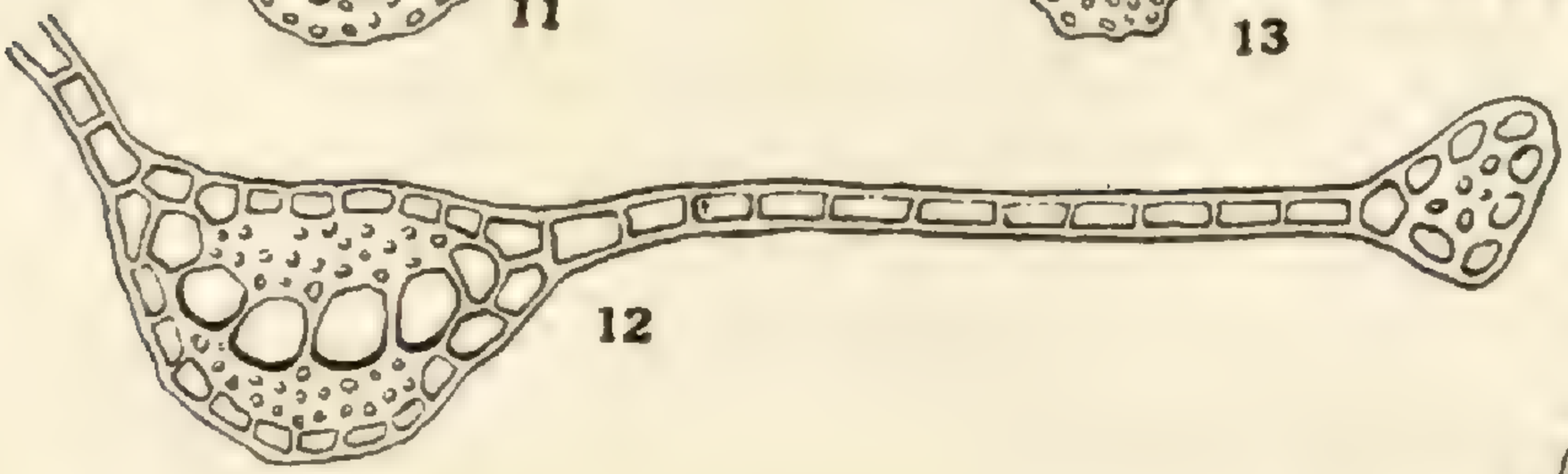

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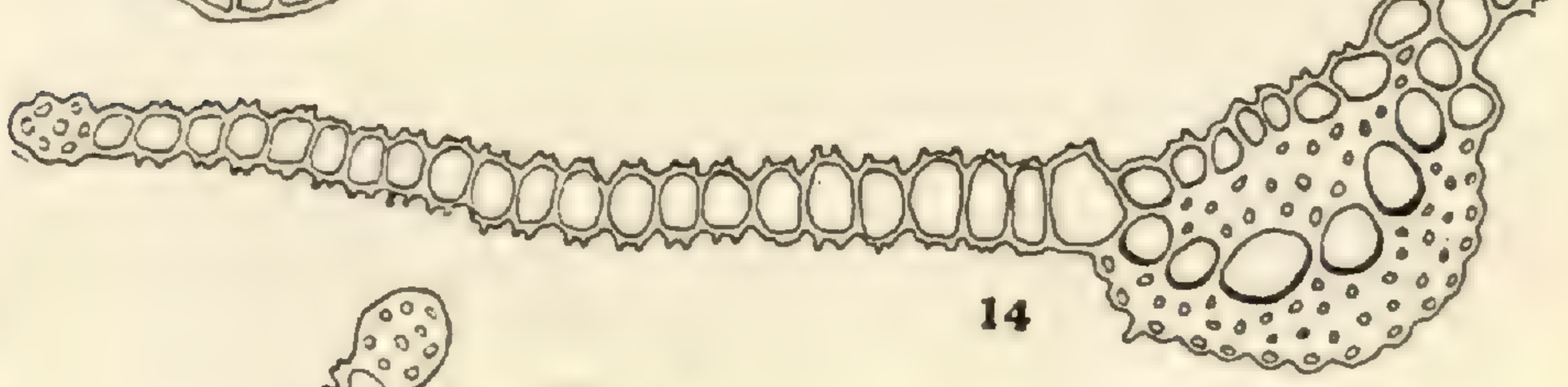

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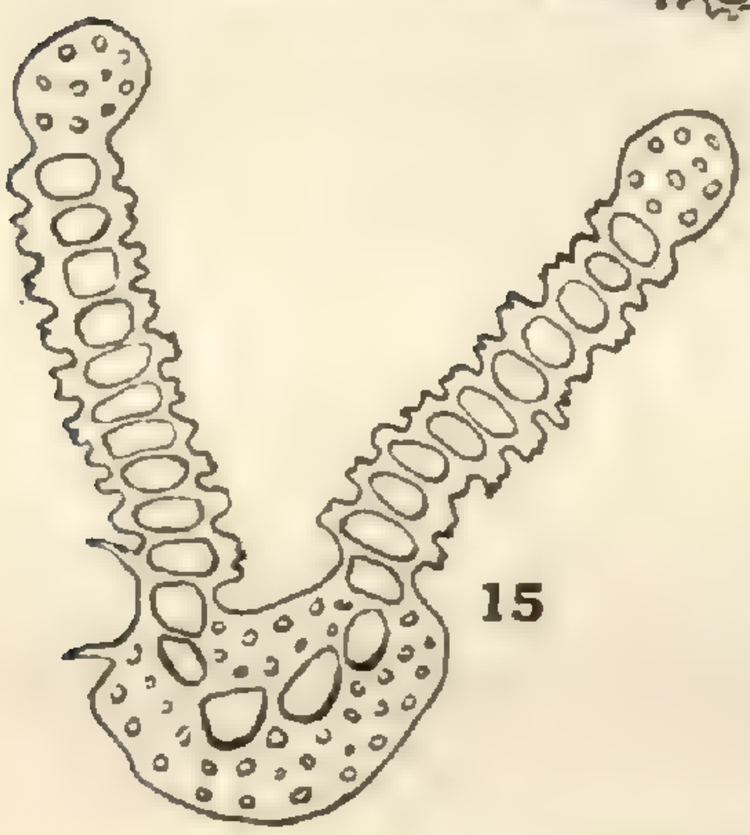

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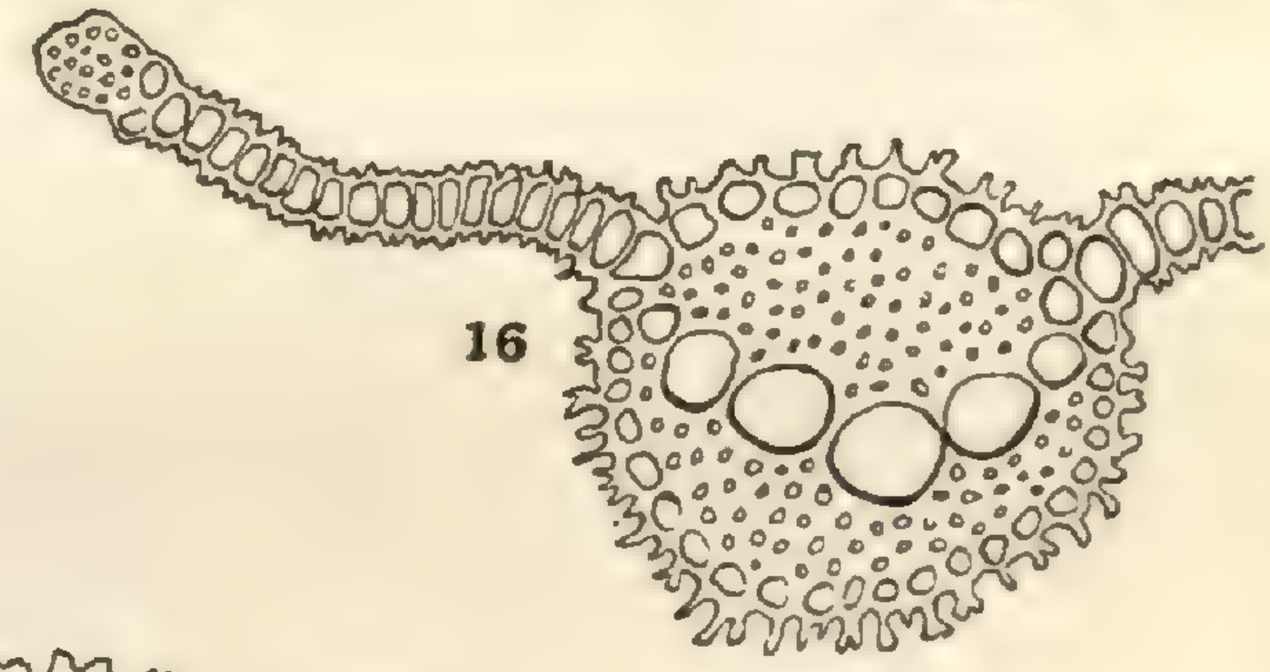

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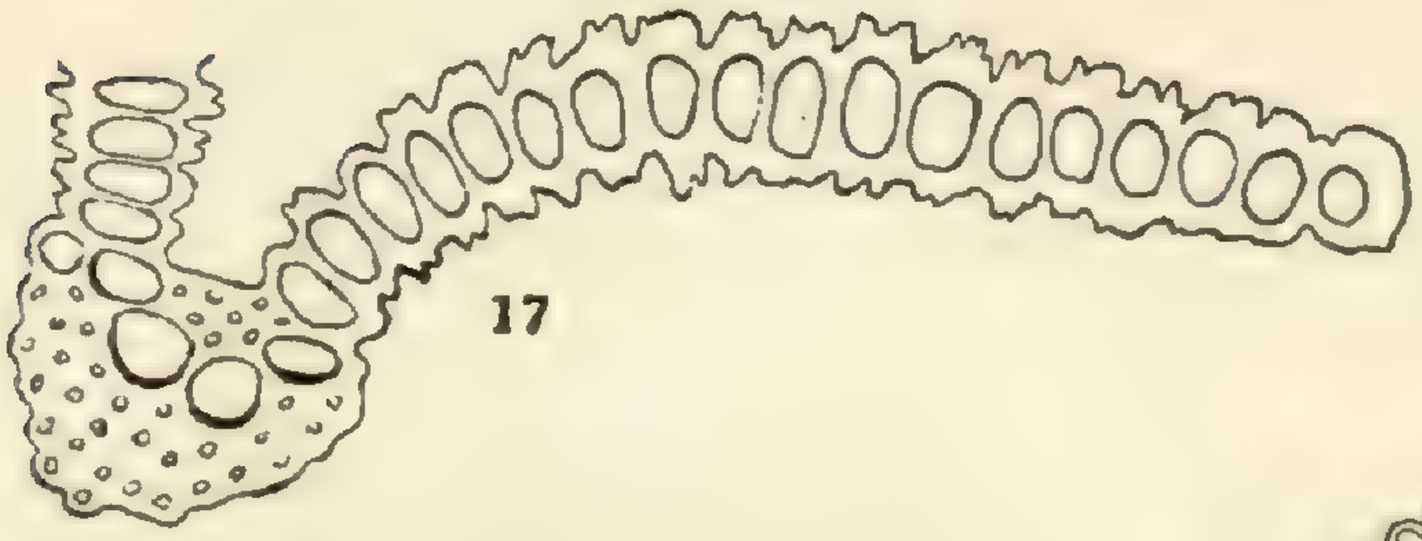

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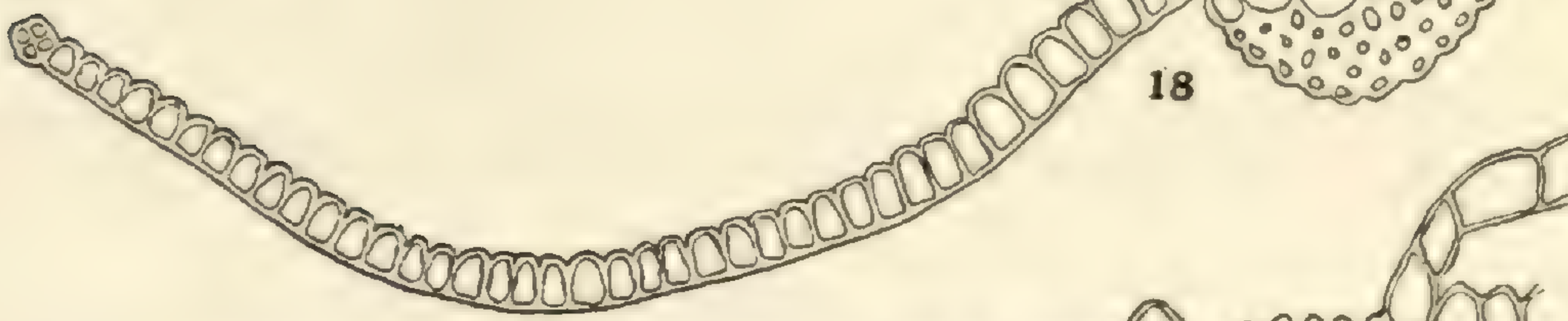

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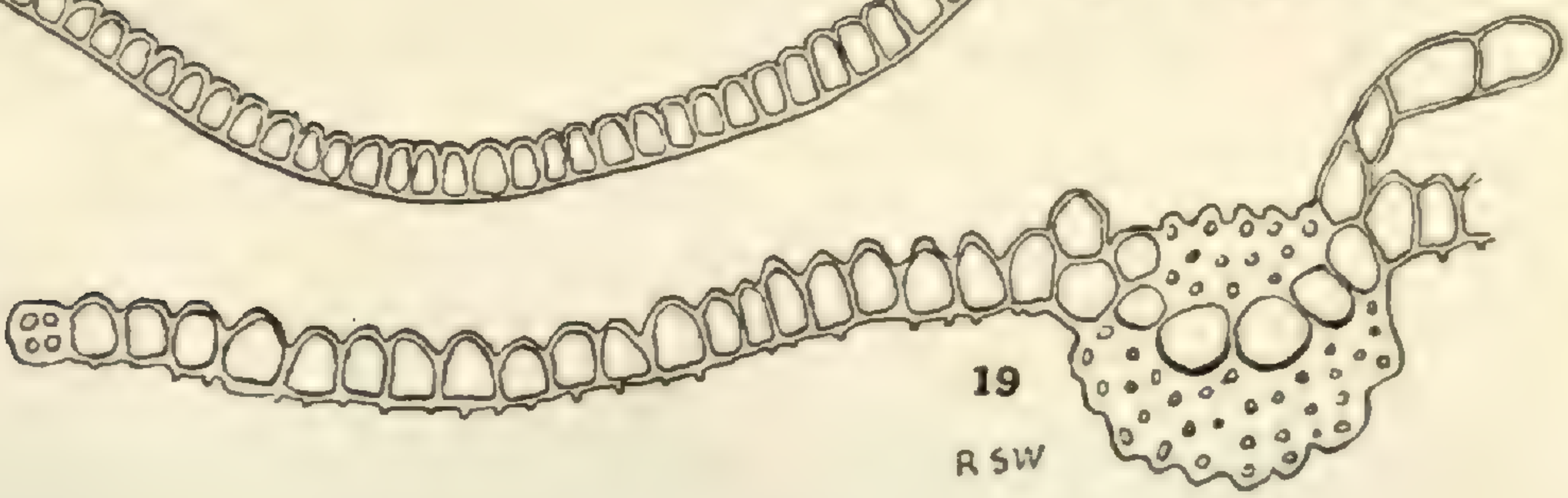

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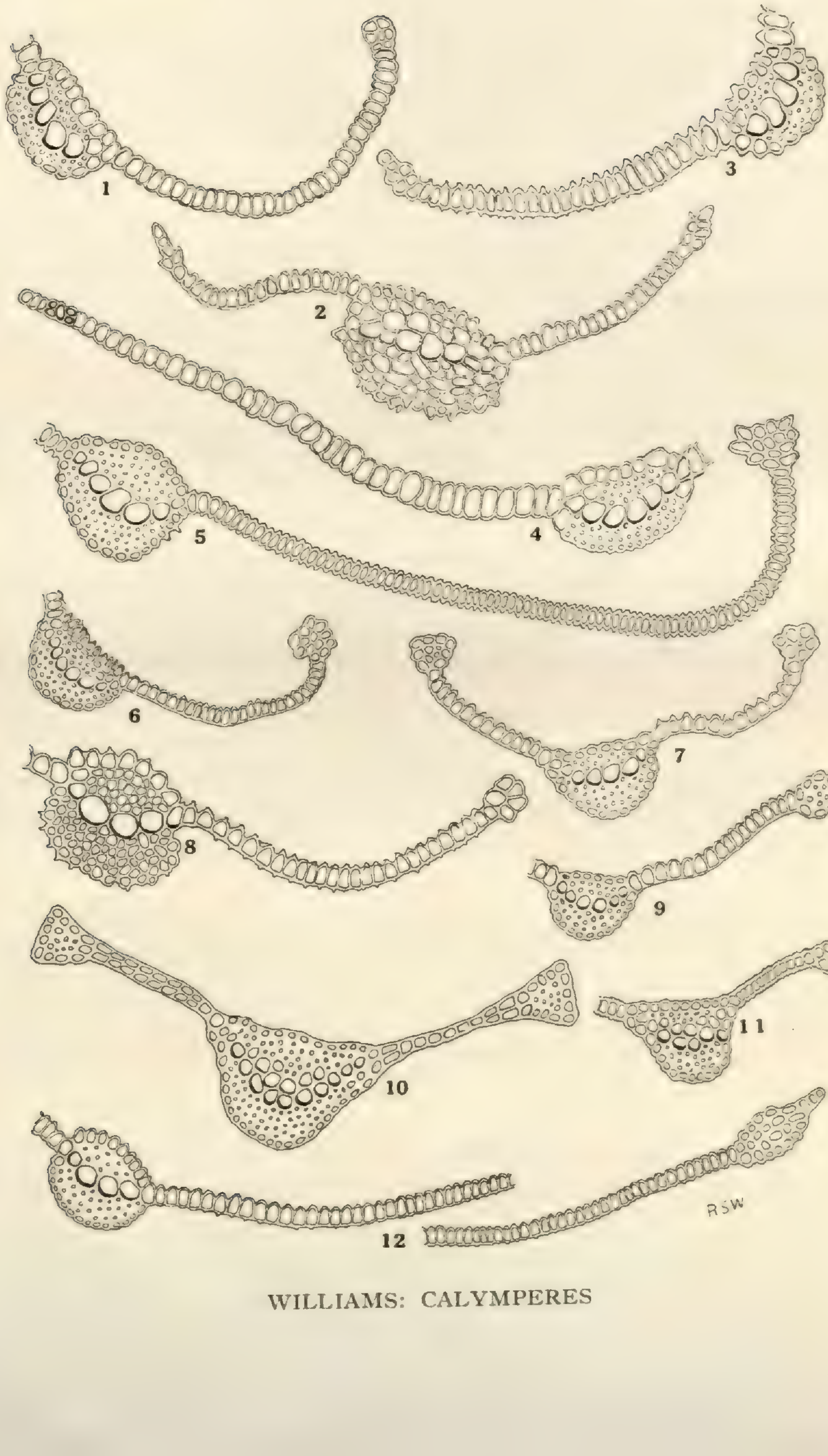

WILLIAMS: CALYMPERES

Vol. 47 No. 10

BULLETIN

OF THE

TORREY BOTANICAL CLUB

OCTOBER, 1920

Phytogeographical notes on the Rocky Mountain region

IX. Wooded formations of the Montane Zone of the Southern Rockies

P. A. RYDBERG

The Montane or Canadian Zone extends in Central Colorado approximately between the altitudes of 2,500 and 3,000 m. In the upper part of the zone naturally many of the Subalpine plants are common and the lower part has been invaded by those of the foothills and plains. Many of these plants have been omitted in this discussion. As the Montane and Subalpine Zones are predominantly wooded, the plant associations are somewhat similar. In the open lands or grass-formations they are more unlike so far as the composition of the vegetation is concerned, the Montane being more like the plains and mesas of the Submontane Zone, and the Subalpine more like the Alpine Zone.

The principal forest trees of this zone are the following:— bull pine (*Pinus scopulorum*), lodge-pole pine (*P. Murrayana*), limber pine (*P. flexilis*), Douglas fir (*Pseudotsuga mucronata*), Engelmann spruce (*Picea Engelmannii*), Colorado blue spruce (*P. Parryana*), balsam fir (*Abies concolor*), narrow-leaved cottonwood (*Populus angustifolia*), balsam poplar (*P. balsamifera*), western black birch (*Betula fontinalis*), Rocky Mountain alder (*Alnus tenuifolia*), and smooth maple (*Acer glabrum*). These have been discussed in a previous paper.* To these may be added several species of willow, hawthorn, and chokecherry, which

* Bull. Torrey Club 42: 11–25. 1915.

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belong principally to the foothills. The following wooded formations may be distinguished, though elements of two or more are often mixed.

I. PINE FOREST

This consists mostly of a mixture of *Pinus scopulorum*, *Apinus flexilis* and *Pseudotsuga mucronata*. In some places, however, one or another of these species is predominant. This formation is limited mostly to the south slopes of the mountains, which are drier and hotter and where the soil is rather poor.

The last one of the three species mentioned seems to be more indifferent, however, to soil and moisture than the others, being found on the north as well as on the south slopes and associating with the pines as well as with the spruces, balsams, and aspens. To the three species are added in the northern part of the Southern Rockies the lodge-pole pine, *Pinus Murrayana*. In some places this forms pure stands, especially on burnt over areas, since it germinates readily and is quick in its growth.

Of the trees belonging to this formation, none is transcontinental or common to the Rockies and the Eastern Canadian Zone, three are common to the Rockies and the Pacific Highlands and one is endemic. Among the shrubs and herbs all four categories are found. As the transcontinentals and the eastern plants act much the same they will be treated together as an eastern element. Those marked "†" are found in the Southern Rockies only, not in the Northern. The nomenclature throughout follows the writer's "Flora of the Rocky Mountains and Adjacent Plains," New York, 1917.

1. TREES

a. Western

Pinus Murrayana — *Pseudotsuga mucronata*
Apinus flexilis

b. Endemic

Pinus scopulorum

2. SHRUBS

a. Eastern or transcontinental

Rubus pubescens — *Lepargyraea canadensis*

Chamaepericlimenum canadense
Arctostaphylos Uva-ursi
Viburnum pauciflorum
Linnaea americana

b. Western

Odostemon Aquifolium
Ribes viscosissimum
Pachystima Myrsinites
Ceanothus velutinus
Gaultheria humifusa
Arctostaphylos platyphylla†

c. Endemic

Ceanothus Fendleri†
Vaccinium oreophilum

3. HERBS

a. Eastern or transcontinental

Oryzopsis asperifolia
Cinna latifolia
Avena striata
Poa compressa
Streptopus amplexifolius
Coeloglossum bracteatum
Lysiella obtusata
Peramium ophioides
Peramium decipiens
Cytherea bulbosa
Corallorrhiza multiflora
Viola Selkirkii
Viola renifolia
Viola canadensis
Aralia nudicaulis
Moneses uniflora
Pyrola asarifolia
Pyrola elliptica
Pyrola chlorantha
Erxlebenia minor
Ramischia secunda
Monotropa uniflora
Veronica serpyllifolia
Botrychium Lunaria
Botrychium neglectum
Thelypteris Dryopteris
Pteris aquilina

b. Western

Oryzopsis Bloomeri
Poa Olneyae
Piperia unalaschensis
Ophrys nephrophylla
Atragene columbiana
Actaea arguta
Ozomelis stauropetala
Micranthes arguta
Osmorrhiza obtusa
Chimaphila occidentalis
Pyrola picta
Pterospora Andromedea
Razoumofskya americana
Razoumofskya Douglasii
Arnica cordifolia
Hieracium albiflorum

c. Endemic

Stipa Porteri†
Stipa Richardsonii
Calamagrostis Scribneri
Poa tricholepis†
Anticlea coloradensis†
Disporum trachycarpum
Trautvetteria media†
Atragene tenuiloba
Actaea viridiflora†
Ozomelis stenopetala†
Ozomelis Parryi†
Drymocallis fissa
Thermopsis pinetorum†
Thermopsis diversicarpa†
Atelophragma aboriginum
Atelophragma Macounii
Aragallus Richardsonii
Hedysarum boreale
Viola scopulorum.
Osmorrhiza intermedia
Primula Parryi
Androsace pinetorum†
Pentstemon secundiflorus†
Pentstemon virens†
Erigeron superbus†
Anaphalis subalpina
Arnica pumila
Arnica sylvatica†
Notholaena Fendleri†
Selaginella Underwoodii†

II. SPRUCE FOREST

This is mostly confined to the north slopes of the mountains, which are much cooler and moister than the south slopes. As in the Subalpine Zone, the principal tree is the Englemann spruce, *Picea Engelmannii*. In some places this forms pure stands but usually it is mixed with the balsam fir, *Abies concolor*, the Colorado blue spruce, *Picea Parryana*, and the Douglas fir, *Pseudotsuga mucronata;* and, in the northern part, sometimes with the lodge-pole pine, *Pinus Murrayana*. The undergrowth is much the same as in the Pine Forest, and no attempt has been made to distinguish the undergrowth of the Pine Forest from that of the Spruce Forest.

III. ASPEN GROVES

These are found on richer more gentle slopes, both on the south and the north side of the mountains, but on the former only where there is a certain amount of moisture. The principal tree is the quaking aspen, *Populus tremuloides*, which I count as a transcontinental tree, as the western form, *P. aurea* Tidestrom, is so closely related to the eastern. The trees of the southern Rockies belong evidently to the latter, but in the Northern Rockies it is unknown where the range of one ends and that of the other begins. The vegetation consists mainly of the following plants:

1. TREES AND SHRUBS

a. Eastern and transcontinental

Populus tremuloides
Salix Bebbiana
Betula papyrifera
Rosa Bourgeauiana
Distegia involucrata

b. Western

Salix Scouleriana
Ribes viscosissimum
Rubacer parviflorum
Rubus melanolasius
Sorbus scopulina
Vaccinium scoparium

c. Endemic

Salix perrostrata
Edwinia americana†
Ribes coloradense†
Ribes Wolfii†
Opulaster glabratus†
Sericotheca microphylla†
Rosa Engelmannii
Rosa melina†
Rosa Woodsii
Sambucus microbotrys†
Sambucus melanocarpa

2. HERBS

a. Eastern and transcontinental

Phleum alpinum
Agrostis oreophila
Avena striata
Danthonia spicata
Poa crocata
Bromus Richardsonii
Agropyrum Richardsonii
Vagnera stellata
Ranunculus micranthus
Fragaria americana
Tium alpinum
Viola canadensis
Heracleum lanatum
Aralia nudicaulis
Pedicularis canadensis
Galium boreale
Erigeron droebachiensis
Botrychium simplex
Botrychium neglectum
Botrychium virginianum
Botrychium silaifolium
Polystichum Lonchitis

b. Western

Festuca subulata
Elymus glaucus
Veratrum speciosum
Vagnera amplexicaulis
Vagnera liliacea
Trillium ovatum
Thalictrum sparsiflorum
Aquilegia coerulea
Fragaria bracteata
Geranium viscosissimum

Geranium Richardsonii
Hypericum formosum†
Osmorrhiza obtusa
Glycosma occidentalis
Ligusticum tenuifolium
Pseudocymopterus sylvaticus
Conioselinum scopulorum
Polemonium occidentale
Collinsia parviflora
Pedicularis racemosa
Aster Geyeri
Erigeron macranthus
Erigeron speciosus
Erigeron conspicuus
Achillea lanulosa
Polypodium hesperium

c. Endemic

Stipa Scribneri†
Oryzopsis micrantha
Poa Vaseyana†
Poa longipedunculata
Festuca sororia†
Agropygron Richardsonii
Anticlea coloradensis†
Lilium montanum
Disporum trachycarpum
Alsine Curtisii
Silene Scouleri†
Silene Hallii†
Thalictrum venulosum
Thalictrum megacarpum
Thalictrum Fendleri†
Thalictrum stipitatum†
Viorna Scottii†
Viorna Jonesii
Atragene tenuiloba
Aquilegia elegantula†
Delphinium Barbeyi†
Aconitum columbianum
Sophia incisa
Sophia procera
Heuchera parviflora
Potentilla jiincunda
Fragaria glauca
Drymocallis fissa
Sieversia grisea
Sieversia ciliata
Lupinus alpestris
Lupinus pulcherrimus
Lupinus humicola
Atelophragma Macounii
Homalobus oblongifolius†
Aragallus deflexus
Hedysarum marginatum†
Lathyrus laetevirens†
Lathyrus leucanthus†
Lathyrus arizonicus†
Ligusticum Porteri†
Ligusticum brevilobum†
Ligusticum affine
Harbouria trachypleura†
Pseudocymopterus montanus†
Pseudocymopterus tenuifolius†
Pseudocymopterus multifidus†
Conioselinum coloradense†
Polemonium delicatum†
Polemonium Archibaldae†
Polemonium molle†
Polemonium robustum†
Polemonium foliosissimum†
Mertensia ciliata†
Castilleja Crista-galli
Castilleja cognata†

Castilleja confusa
Castilleja rhexifolia
Castilleja trinervis
Pedicularis Parryi
Pedicularis crenulata†
Galium flaviflorum†
Oreochrysum Parryi†.
Eucephalus wasatchensis†
Eucephalus glaucus†
Eucephalus formosus†
Aster adscendens
Erigeron yellowstonensis
Erigeron subtrinervis
Antennaria viscidula
Anaphalis subalpina
Helianthella Parryi†
Arnica macilenta†

IV. POPLAR GROVES

These are found in the narrower valleys and cañons, where there is a certain amount of moisture, but where the ground is comparatively well drained. The principal tree is the narrow-leaved poplar or cottonwood, *Populus angustifolia*. Another common tree is *Salix Scouleriana*, and Young* has called this formation the *Populus angustifolia—Salix Nuttallii* Formation.

Another common tree is the smooth maple, *Acer glabrum*. The balsam poplar, *Populus balsamifera*, has been collected in a few places in Colorado, and the canoe birch, *Betula papyrifera* (*B. Andrewsii*), has been collected in one cañon. Some of the evergreens have also partly invaded this formation, as *Pseudotsuga mucronata* and *Abies concolor*, and a few species of hawthorn are found in the lower part of the zone. In the Foothills (Submontane Zone) the narrow-leaved cottonwood is replaced mostly by *Populus acuminata* and *P. Sargentii*. The undershrub and herbaceous vegetation contains many species found in the Aspen Groves.

1. TREES AND SHRUBS

a. Eastern

Populus balsamifera
Salix Bebbiana
Betula papyrifera
Dasiphora fruticosa

b. Western

Pseudotsuga mucronata
Salix Scouleriana
Ribes viscosissimum
Cercocarpus ledifolius
Rubacer parviflorum
Rubus melanolasius

* Bot. Gaz. 44: 334–336. 1907.

c. Endemic

Populus angustifolia
Salix lutea
Salix padophylla
Salix perrostrata
Betula fontinalis
Edwinia americana†
Ribes coloradense†
Ribes Wolfii†
Opulaster monogynus†
Opulaster glabratus†
Sericotheca microphylla†
Rosa Engelmannii
Rosa melina
Rosa Woodsii
Sambucus microbotrys†
Sambucus melanocarpa
Sambucus neomexicana†

2. HERBS

a. Eastern or transcontinental

Torresia odorata
Phleum alpinum
Agrostis hyemalis
Calamagrostis canadensis
Dactylis glomerata
Poa crocata
Festuca rubra
Bromus ciliatus
Vagnera stellata
Chenopodium Botrys
Blitum capitatum
Claytonia virginica
Moeringia lateriflora
Moeringia macrophylla
Fragaria americana
Prunella vulgaris
Specularia perfoliata
Aster laevis
Erigeron droebachiensis
Filix fragilis

b. Western

Calamagrostis luxurians
Bromus polyanthus
Elymus glaucus
Ranunculus Douglasii
Ranunculus Bongardi
Aquilegia coerulea
Delphinum Nelsonii
Fragaria bracteata
Drymocallis corymbosa
Thermopsis montana
Lupinus tenellus
Geranium Richardsonii
Geranium viscosissimum
Glycosma occidentalis
Apocynum ambigens
Castilleja lancifolia
Erigeron macranthus
Aster Geyeri
Achillea lanulosa
Senecio pseudaureus

c. Endemic

Poa reflexa
Agropyron Richardsonii
Lilium montanum
Disporum trachycarpum

Chenopodium Fremontii
Silene Scouleri
Thalictrum megacarpum
Atragene tenuiloba
Ranunculus Earlei†
Delphinum robustum†
Delphinum elongatum
Delphinum ramosum†
Sophia leptophylla
Sophia incisa†
Sophia procera†
Fragaria glauca
Lupinus floribundus†
Lupinus parviflorus
Lupinus pulcherrimus
Lupinus humicola
Homalobus tenellus
Lathyrus brachycalyx†
Lathyrus leucanthus†
Lathyrus arizonicus†
Sidalcea candida†
Oxypolis Fendleri†
Apocynum scopulorum
Polemonium foliosissimum†
Hydrophyllum Fendleri†
Agastache pallidiflora†
Agastache urticifolia
Moldavica parviflora
Scrophularia occidentalis
Castilleja Crista-galli
Castilleja rhexifolia
Castilleja sulphurea
Pedicularis Grayi†
Galium flaviflorum†
Valeriana micrantha
Eucephalus glaucus†
Aster ciliomarginatus
Aster adscendens
Erigeron yellowstonensis
Erigeron superbus†
Helianthella quinquenervis
Anaphalis subalpina
Arnica subplumosa

V. ALDER–WILLOW SWAMPS

These are found in the wetter parts of the valleys, where the drainage is rather poor. They contain many of the species found in the preceding formation but also many belonging to the Sedge Bog. The most important woods belonging to the formation are the Rocky Mountain alder, *Alnus tenuifolia*, the western black birch, *Betula fontinalis*, and several species of willows. In the upper part of the zone, the formation becomes more and more like the willow bogs of the Subalpine Zone.*

1. TREES AND SHRUBS

a. Eastern

Salix chlorophylla *Salix cordata*

* See Bull. Torrey Club 44: 449–450. 1917.

Betula glandulosa
Dasiphora fruticosa
Distegia involucrata

b. Western

Salix Scouleriana
Salix glaucops
Almus tenuifolia
Kalmia microphylla

c. Endemic

Salix padophylla
Salix monticola
Salix Wolfii
Salix irrorata†
Salix perrostrata
Salix pachnophora†
Salix brachycarpa
Betula fontinalis
Svida instolonea
Negundo Kingii†
Sambucus microbotrys†
Sambucus melanocarpa
Sambucus neomexicana†

2. HERBS

a. Eastern and transcontinental

Calamagrostis canadensis
Panicularia nervata
Eleocharis palustris
Eleocharis acicularis
Streptopus amplexifolius
Alsine alpestris
Alsine crassifolia
Alsine borealis
Sisymbrium Nasturtium-aquaticum
Cardamine pennsylvanica
Geum rivale
Heracleum lanatum
Mimulus moschatus
Veronica americana
Elephantella groenlandica
Senecio pauciflorus
Nabalus racemosus
Equisetum arvense

b. Western

Poa leptocoma
Elymus glaucus
Veratrum speciosum
Limnorchis stricta
Limnorchis viridiflora
Limnorchis borealis
Thalictrum sparsiflorum
Ranunculus Douglasii
Ranunculus Bongardi
Trollius albiflorus
Parnassia fimbriata
Geum oregonense
Circaea pacifica
Mimulus Langsdorfii
Mimulus Lewisii
Pedicularis bracteosa
Galium subbiflorum
Senecio triangularis

Senecio pseudaureus
Athyrium cyclosorum

c. Endemic

Poa reflexa
Panicularia pauciflora
Juncus truncatus
Allium brevistylum
Disporum trachycarpum
Limnorchis purpurascens†
Corallorrhiza ochroleuca
Corallorrhiza Vreelandii†
Rumex subalpinus†
Alsine Curtisii†
Thalictrum megacarpum
Thalictrum Fendleri†
Ranunculus Earlei†
Caltha rotundifolia†
Aconitum columbianum
Cardamine cordifolia†
Cardamine infausta†
Parnassia rivularis†
Geum decurrens†
Sidalcea candida†
Phymosia Crandallii†
Phymosia rivularis
Phymosia grandiflora†
Mertensia ciliata†
Scutellaria Brittonii†
Castilleja sulphurea
Pedicularis Grayii†
Galium flaviflorum†
Aster Canbyi†
Rudbeckia ampla
Senecio nephrophyllus†

VI. COPSES

Besides the shrubby willows included in the preceding formation, there are also shrubberries on dryer ground. These are found partly along the edges of the Aspen and Poplar Groves, the Willow Swamps and even the pinewoods, partly on dryer river-banks, and partly on the hillsides. Though the species of shrubs are not so many, the herbaceous flora associated with them is richer in species than that of either the woods or the meadows. In fact these copses contain many belonging to either and besides many of its own. Many of those belonging mainly to the woods or to the meadows are here omitted.

1. SHRUBS

a. Eastern

Dasiphora fruticosa

b. Western

Cerocarpus ledifolius
Rubacer parviflorum
Rubus melanolasius
Vaccinum scoparium

c. Endemic

Salix perrostrata
Salix brachycarpa
Atragene pseudoalpina†
Edwinia americana†
Edwinia macrocalyx†
Fendlera falcata†
Opulaster monogynus†
Opulaster alternans†
Chamaebatiaria Millefoliium†
Sericotheca microphylla
Cercocarpus montanus
Oreobatus deliciosus†
Rosa melina†
Rosa aciculata†
Rosa manca†
Amelanchier oreophila†
Amelanchier Bakeri†
Amelanchier prunifolia†
Ceonothus velutinus
Vaccinium oreophilum

2. HERBS

a. Eastern

Panicum huachucae
Allium sibiricum
Vagnera stellata
Vagnera stellata
Bilderdykia Convolvulus
Moehringia latifolia
Moehringia macrophylla
Vicia trifida
Vicia americana
Xanthoxalis Bushii
Apocynum androsaemifolium
Clinopodium vulgare†
Pedicularis canadensis
Galium boreale
Specularia perfoliata

b. Western

Melica bella
Hesperochloa Kingii
Aquilegia coerulea
Lithophragma bulbifera
Lithophragma parviflora
Drymocallis corymbosa
Drymocallis glandulosa
Lupinus tenellus
Thermopsis montana
Linum Lewisii
Glycosma occidentalis
Apocynum ambigens
Gilia aggregata
Gilia pulchella
Hydrophyllum capitatum
Phacelia sericea
Lappula floribunda
Collinsia parviflora
Castilleja lancifolia
Erigeron macranthus
Balsamorrhiza sagittata
Achillea lanulosa
Artemisia Michauxiana

c. Endemic

Stipa Scribneri†
Orzyopsis micranatha
Poa reflexa
Poa rupicola
Agropyrum Richardsonii
Disporum trachycarpum
Lilium montanum
Polygonum Engelmannii
Silene Scouleri
Atragene pseudoalpina†
Capnoides Brandegei†
Sophia magna†
Sophia andrenarum
Sophia leptostylis†
Draba spectabilis†
Draba Helleriana†
Hesperidanthus linarifolius†
Heuchera bracteata†
Heuchera Hallii†
Heuchera utahensis†
Heuchera parvifolia
Potentilla glaucophylla
Fragaria glauca
Lupinus floribundus†
Lupinus parviflorus
Tium scopulorum†
Homolobus decurrens†
Homolobus tenuifolius
Hedysarum utahense†
Lathyrus laetivirens
Lathyrus leucanthus†
Lathyrus arizonicus†
Viola montanensis
Ligusticum brevilobum†
Amarella heterosepala†
Amarella scopulorum
Dasystephana Parryi†
Phacelia ciliata
Dasystephana affinis
Dasystephana Forwoodii
Apocynum scopulorum
Polemonium albiflorum†
Hydrophyllum Fendleri†
Mertensia lanceolata
Agastache pallidiflora†
Agastache urticifolia
Moldavica parviflora
Scrophularia occidentalis
Penstemon strictus†
Penstemon unilateralis†
Penstemon Rydbergii
Penstemon virens
Penstemon Leonardi†
Penstemon Torreyi†
Castilleja Crista-galli
Castilleja rhexifolia
Pedicularis crenulata
Valeriana trachycarpa†
Valeriana micrantha
Coleosanthus umbellatus†
Coleosanthus albicaulis†
Macronema obtusum†
Eucephalus glaucus
Aster subgriseus†
Aster ciliomarginatus
Aster adscendens
Erigeron incanescens†
Erigeron Smithii
Helianthella Parryi†
Senecio ambrosioides
Senecio multicapitatus†
Heteropleura Fendleri†
Agoseris agrestis†

VII. SAGEBRUSH

To the woody formations may also be added the Sagebrush lands. These are more characteristic of the Submontane Zone, but are also found in the Montane Zone above as well as in the Sonoran below. The most important shrub is *Artemisia tridentata*, which is found in all three zones. So also is *A. cana*, but the other sagebrushes are most common in the higher zones. As the sage lands are open formations, the undergrowth is mostly the same as in the dry valleys and on the tablelands. Only a few plants rather characteristic of this formation will be mentioned.

1. SHRUBS

Chrysathamnus filifolius
Artemisia cana
Artemisia tridentata
Artemisia nova
Artemisia tripartita

2. HERBS

Eriogonum cernuum
Penstemon cyathophorus
Penstemon xylus
Penstemon teuchrioides
Castilleja flava

NEW YORK BOTANICAL GARDEN

A method of preparation and some properties of a starch gel

Cornelia Lee Carey

Much of the work on starch has been on saccharification and very little on the colloidal properties, particularly those of the starch gel. Although starch in the gel condition does not exist in nature, it is interesting both from a colloidal chemical standpoint and also in relation to carbohydrate gels such as agar or cellulose.

It is difficult to prepare a starch gel which is stiff enough to be handled without breaking and crumbling, and it is almost impossible to make good gels of very high concentration, such as the one used here, by the usual procedure. It was with this idea in view that the following method was used. A 100 grams of commercial corn starch were well mixed with 150 c.c. of cold distilled water, and the mixture then poured into covered petri dishes. Enough starch solution was poured into each dish so that the bottom was just covered. A number of these dishes were then put in the autoclave for thirty minutes at a temperature ranging from 105° to 110° C. When still warm the starch was cut into strips. They were then put over the radiator to dry, later in the oven at 35° C., and finally dried in a desiccator over calcium chloride to constant weight. The starch prepared in this manner does not break on handling and when placed in water, at low temperatures, is only very slightly soluble. When completely dry it is somewhat transparent and tough. The transparency disappears again after standing in water for twenty four hours, but even after this it ir still fairly tough. Strips of this starch were weighed, put in 100 c.c. of distilled water and left for twenty-four hours at different temperatures. Surface water was removed by dipping the strips quickly into alcohol and ether and blotting on filter paper. They were then weighed to determine the amount of water adsorbed. In all cases the starch kept its shape and at low temperatures was hard and firm.

The water in which the starch strips had been standing turned

blue with iodine, but the amount of starch dissolved at low temperatures was not large. This increases as the temperature rises. Strips of the starch gel were placed in 100 c.c. of water and allowed to stand for twenty-four hours. An aliquot portion of the liquid was taken, evaporated and dried to constant weight in a desiccator. TABLE I gives the results, taken from only one determination in each case. In plotting the graph as indicated by the above figures it is apparent that there is a very sudden rise in the amount of the gel which passes into solution at 70° C. At the lower temperatures the correction would be negligible as is shown in TABLE II. The correction has been applied tentatively for the reason named above, since it would require more than one determination to determine it definitively. In any event it is obvious that the adsorption of water per gram starch gel would actually be even greater than as given in the tables at the end of this paper. It seems possible that the substance dissolved in the water does not do so immediately, but only on standing. No work, however, was done to determine this. The liquid at 90° C. and also those at lower temperatures gave no test for reducing sugars with Fehling's solution. At the higher temperatures the strips became larger and softer than at the lower but kept their shape.

TABLE I

	Temperature degrees Centigrade			
	35	70	80	90
Dry weight of strip in grams	2.064	0.800	0.679	0.664
Volume of water remaining after adsorption, cc.	97.768	97.432	97.634	97.402
Starch residue in 25 cc. of above water, in grams	0.001	0.006	0.016	0.030
Total weight of starch residue, in grams	0.039	0.024	0.061	0.117
Per cent weight of original strip dissolved	0.19	2.90	9.06	17.60

A microscopical view of a section of one of these starch strips showed that it did not have a homogeneous structure but was made of partially decomposed starch grains with a jelly-like substance between them which cements or holds them together. These partly swollen grains appeared unchanged even after boiling ten minutes in water. There may have been a slight increase in size, but no measurements were taken to determine this. It is the opinion of the writer that the starch grains only

partly swelled, at the temperature at which the gel was made, due to lack of water. It will be remembered that the gel was highly concentrated, $66^2/_3$ per cent, and it may be that swelling goes on forming a paste and leaving the grains only slightly changed, due to the insufficient supply of water present. A 10 per cent gel made by mixing starch and cold water and adding boi ing water to it contains empty sacs in the gelatinous mass. A 2 per cent gel after boiling five minutes showed these empty envelopes. These are probably the individual covers of the starch grains. Whether further disintegration takes place in the grains of the gel used in this work on standing in water at higher temperatures is not known, but investigation will be carried on along this phase of the problem.

Meyer (5), in his work on starch, observed these sacs. The early stages in swelling correspond to those seen in the gel used here. In this formation, according to him, the swelling continues until the sac is formed. In the beginning striations appear which disappear when the sacs become larger. Later the walls of the sacs wrinkle and when swelling is complete the walls of these collapsed sacs consist of a gel which is made of amicroscopic drops. Meyer also worked with corn starch. He prepared it by first mixing the starch with cold, and then with boiling, water. When the vessel containing the starch was placed in boiling water for five minutes all the grains were swollen and the sacs floated freely in the sol. The partly swollen grains, observed by the writer, appeared much as Meyer has described them. The contents were striated, the stripes running out from the center, and in the weaker gels the sacs seemed empty.

The gel is fairly resistant to heat. When newly made and while still hot, if boiled in water for fifteen minutes, only a small part went into solution. If the gel is allowed to set entirely, the amount dissolving becomes less. Gels fully dehydrated when boiled fifteen minutes kept their shape. They dissolved somewhat, however, as the liquid gave the characteristic blue color with iodine. If a 10 per cent sol, when still hot, (i.e. immediately after making) is put into boiling water, it dissolves. When the same gel is set and then boiled fifteen minutes only part of it goes into solution. It would appear from this that the setting of the sol is what makes

it partly irreversible at the temperature of boiling water. The higher the concentration of the sol the quicker the setting takes place, so that the starch used in this work was practically set when removed from the autoclave. This agrees with examples given by Meyer (5), showing that the setting of a sol at a certain temperature is more rapid the higher the concentration.

Maquenne and Roux (3, 4) found that ordinary starch paste contained 80–90 per cent amylocellulose and the rest amylopectin. This they concluded from the results of iodine and saccharifying tests. They considered the geling properties of starch were due to the amylopectin. The amylocellulose was partly soluble in boiling water and completely liquified, according to Roux (6), in excess of water at 150° C. and had no geling power. At 90° C. 18 per cent of the gel goes into solution, according to the work of the writer. It may be that this is all amylopectin of Maquenne.

Taylor (7, p. 127) mentions the fact that starch sols are like silicic acid sols in their behavior, but does not state in what manner. The gel, however, seems to simulate more closely the elastic gels of agar and gelatine than the rigid one of silicic acid. Even these elastic gels have to be heated to a higher temperature than that at which gelation occurred before they will again become sols. The geling and melting points, in the case of gelatine, however, vary with the concentration and are also affected by organic substances and salts.

The general averages of the determinations given in the tables at the end of this paper, under APPENDIX, are shown in TABLE II, below. In the work carried on by the writer, with the range of temperatures used, the higher the temperature the more water was absorbed. Thus it is evident from the following figures there was no maximum point above which the adsorption decreased, at least up to 90° C. For at 8.5–10.5° C. the average adsorption is 0.864 grams water per gram dry starch, whereas at 90° C. it has risen to 3.713 grams of water, an increase of over four times that at about 8° C. As the temperature was raised the size of the strips increased upon swelling; they became softer and of a less tough and firm consistency. In some of the solutions at high temperatures there were minute shiny particles, the nature of which was not determined.

TABLE II

GENERAL AVERAGES FROM TABLES III–XI (SEE APPENDIX)

Temperature degrees Centigrade	Adsorption water per gram dry starch gel on basis of original weight	Adsorption water per gram, corrected according to TABLE I
8.5–10.5	0.864	correction negligible
17.5	0.896	" "
24	0.916	" "
35	1.140	1.142
50	2.426	2.448
60	2.807	2.865
70	3.153	3.274
80	3.427	3.768
90	3.713	4.411

In MacDougal's work with artificial biocolloid mixtures (1), mainly of agar but containing some protein, an increase in the total amount of swelling was found to a maximum point between 39° and 46° C. MacDougal (2) has also shown a greater swelling of agar than of gelatine in distilled water at the same temperature, and in mixtures of the two the swelling increased as the percentage of agar in the mixture was increased. From these results, and also from those shown in this paper, it would appear that at least carbohydrate gels behave somewhat similarly.

This increased adsorption with rise in temperature does not agree with Taylor (7, p. 155), who states that, according to LaChatelier's theorem, heat diminishes and cold and pressure increase imbibition. But Meyer (5) refers to the fact that gels dried in the air will swell again if put into water, the swelling being greater the higher the temperature of the water. The temperatures at which the writer's experiments were performed varied slightly from that taken as the average, but in no case was it enough to be noticeable in the amounts of water adsorbed.

The preparation of this starch gel was undertaken with the idea of obtaining a pure carbohydrate gel, which on account of its hydrative capacity would be suitable for experimentation under various conditions. In a sense it might be said to simulate a cellulose membrane, but it would be unsafe to carry the comparison too far. Inasmuch as the hydration of organic elastic gels is of fundamental importance in many physiological problems which are attracting great attention today, it has seemed worth while to place on record the results of the above experiments as a contribution to a partial knowledge of some of the properties which

this starch gel presents. The study of such systems becomes of interest, not only on account of the mere increase in size—the swelling which takes place on immersion in water with the implications that such phenomena have as regards growth phenomena—but also on account of its possible relation to problems of metabolism.

Since no chemical analyses were made (except those for reducing sugars in the water in which the strips had stood), the writer cannot say whether any changes took place in the starch due to the temperatures employed, either in the structure of the starch grains or chemically, but simply gives this method as a means of preparing a fairly resistant starch gel which is easily handled.

I wish to thank Dr. Herbert M. Richards for his valuable idea on the method and his helpful suggestions throughout the work, which are greatly appreciated.

BOTANICAL LABORATORY,
BARNARD COLLEGE,
COLUMBIA UNIVERSITY

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APPENDIX

TABLE III

WEIGHT OF WATER ADSORBED BY DRIED STARCH GEL IN GRAMS AT TEMPERATURE FROM 8.55 TO 10.5° C.

Original starch gel taken	After 24 hours in water	Gain	Water adsorbed per gram starch
1.320	2.552	1.232	0.933
1.073	1.937	0.864	0.805
1.107	2.045	0.938	0.847
1.552	2.821	1.269	0.817
1.484	2.743	1.259	0.848
0.932	1.709	0.777	0.833
0.970	1.809	0.839	0.864
1.067	1.984	0.917	0.859
0.741	1.462	0.721	0.973
0.897	1.667	0.770	0.858
			0.864

TABLE IV

WEIGHT OF WATER ADSORBED BY DRIED STARCH GEL IN GRAMS AT TEMPERATURE ABOUT 17.4° C.

Original starch gel taken	After 24 hours in water	Gain	Water adsorbed per gram starch
1.438	2.716	1.278	0.888
1.499	2.781	1.282	0.855
1.032	1.991	0.959	0.929
1.827	3.381	1.554	0.850
0.856	1.692	0.836	0.976
0.903	1.818	0.915	1.013
1.327	2.610	1.283	0.967
1.202	2.350	1.148	0.955
2.013	2.688	1.675	0.832
1.920	3.498	1.578	0.821
1.076	1.951	0.875	0.813
1.396	2.592	1.196	0.856
			0.896

TABLE V

WEIGHT OF WATER ADSORBED BY DRIED STARCH GEL IN GRAMS AT TEMPERATURE ABOUT 24° C.

Original starch gel taken	After 24 hours in water	Gain	Water adsorbed per gram starch
2.642	5.103	2.461	0.932
1.752	3.419	1.667	0.953
1.648	2.719	1.071	0.650
1.497	2.852	1.355	0.905
1.507	3.022	1.515	1.005
1.411	2.816	1.405	0.995
1.425	2.799	1.374	0.964
1.453	2.796	1.343	0.923
			0.916

TABLE VI

WEIGHT OF WATER ADSORBED BY DRIED STARCH GEL IN GRAMS AT TEMPERATURE ABOUT 35° C.

Original starch gel taken	After 24 hours in water	Gain	Water adsorbed per gram starch
1.716	3.680	1.964	1.144
1.531	3.300	1.769	1.155
1.825	3.930	2.102	1.149
1.580	3.306	1.726	1.092
1.564	3.230	1.666	1.065
2.064	4.296	2.232	1.081
1.759	3.843	2.084	1.184
2.001	4.169	2.168	1.081
1.161	2.605	1.444	1.243
1.216	2.686	1.470	1.208
			1.140

TABLE VII

WEIGHT OF WATER ADSORBED BY DRIED STARCH GEL IN GRAMS AT TEMPERATURE ABOUT 50° C.

Original starch gel taken	After 24 hours in water	Gain	Water adsorbed per gram starch
0.519	1.791	1.272	2.450
0.830	2.838	2.008	2.407
0.760	2.535	1.765	2.322
0.895	3.079	2.174	2.429
0.812	2.782	1.970	2.426
0.766	2.655	1.889	2.466
0.726	2.506	1.780	2.451
0.898	3.023	2.125	2.366
0.845	2.935	2.090	2.473
0.618	2.147	1.529	2.474
			2.426

TABLE VIII

WEIGHT OF WATER ADSORBED BY DRIED STARCH GEL IN GRAMS AT TEMPERATURE ABOUT 60° C.

Original starch gel taken	After 24 hours in water	Gain	Water adsorbed per gram starch
0.796	2.983	2.187	2.747
0.350	1.306	0.956	2.731
0.804	2.981	2.177	2.707
0.468	1.744	1.276	2.726
0.592	2.145	1.553	2.623
0.489	1.905	1.416	2.895
0.770	2.860	2.090	2.714
0.670	2.664	1.994	2.976
0.752	3.011	2.259	3.003
0.740	2.921	2.181	2.947
			2.807

TABLE IX

WEIGHT OF WATER ADSORBED BY DRIED STARCH GEL IN GRAMS AT TEMPERATURE ABOUT 70° C.

Original starch gel taken	After 24 hours in water	Gain	Water adsorbed per gram starch
0.468	1.944	1.476	3.154
0.402	1.610	1.208	3.004
0.644	2.622	1.978	3.071
0.513	2.105	1.692	3.298
0.637	2.613	1.976	3.102
0.433	1.866	1.433	3.307
0.809	3.377	2.568	3.171
0.800	3.368	2.568	3.210
0 921	3.785	2.864	3.109
0.595	2.446	1.851	3.107
			3.153

TABLE X

WEIGHT OF WATER ADSORBED BY DRIED STARCH GEL IN GRAMS AT TEMPERATURE ABOUT 80° C.

Original starch gel taken	After 24 hours in water	Gain	Water adsorbed per gram starch
0.656	2.693	2.037	3.105
0.519	2.246	1.727	3.327
0.674	3.056	2.382	3.534
0.968	4.375	3.407	3.519
0.729	3.146	2.417	3.315
0.700	3.058	2.358	3.368
0.600	2.810	2.210	3.683
0.975	4.232	3.257	3.340
0.598	2.748	2.150	3.595
0.679	3.045	2.366	3.484
			3.427

TABLE XI

WEIGHT OF WATER ADSORBED BY DRIED STARCH GEL IN GRAMS AT TEMPERATURE ABOUT 90° C.

Original starch gel taken	After 24 hours in water	Gain	Water adsorbed per gram starch
0.968	4.417	3.449	3.563
0.954	4.462	3.508	3.677
0.588	2.677	2.089	3.552
0.636	2.995	2.359	3.709
0.798	3.849	3.051	3.823
0.736	3.011	2.275	3.091
0.819	3.986	3.167	3.866
0.836	4.076	3.240	3.875
0.752	3.810	3.058	4.066
0.664	3.262	2.598	3.912
			3.713

New species of Uredineae—XII*

Joseph Charles Arthur

The preceding number in this series† was issued in April, 1919. Since that time the work of studying and assorting all of the remaining material in the rust herbarium, not heretofore assigned to acceptable genera and species, has proceeded with the result that a number of forms have been separated as worthy of recognition under distinctive names. These new species, founded for the most part on collections that have long reposed in various herbaria, together with two species that have been passing under erroneous names, are here established. A few species are transferred to other genera, and in three cases where the name was preoccupied new names have been given.

Melampsora americana sp. nov.

O. Pycnia hypophyllous, scattered among the aecia, broadly conic or hemispheric, yellowish or light-brown, rather inconspicuous, subcuticular but extending into and disintegrating the epidermal cells beneath, 80–150 μ broad by 50–90 μ high; ostiolar filaments wanting.

I. Aecia hypophyllous, scattered over part or all of the leaf on yellowish areas, oval or oblong, 0.3–0.8 mm. long, soon naked, pulverulent, at first orange-color, becoming pale-yellow, ruptured cuticle barely noticeable; aeciospores globoid or ellipsoid, 12–18 by 16–23 μ; wall colorless, 1.5–2.5 μ thick, closely and finely but noticeably verrucose.

II. Uredinia hypophyllous, irregularly scattered, usually on yellow spots, round, either very small, 0.1–0.2 mm. across, and pale, or large, 0.2–0.5 mm. across, pulvinate, orange fading to pale-yellow, ruptured epidermis inconspicuous; paraphyses capi-

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* Reprints may be obtained by application to the Botanical Department, Purdue University Agricultural Experiment Station, Lafayette, Indiana, under whose auspices the studies here reported were largely carried out.

† New species of Uredineae I–XI: Bull. Torrey Club (I) **28**: 661–666. 1901; (II) **29**: 227–231. 1902; (III) **32**: 1–8. 1904; (IV) **33**: 27–32. 1906; (V) **33**: 513–522. 1906; (VI) **34**: 583–592. 1907; (VII) **37**: 569–580. 1910; (VIII) **38**: 369–378. 1911; (IX) **42**: 585–593. 1915; (X) **45**: 141–156. 1918; (XI) **46**: 107–125. 1919.

tate or clavate-capitate, 20–30 μ broad in upper part, 30–60 μ long, in strongly capitate forms the wall 4–5 μ thick, obliterating the lumen of the stalk, thicker at apex, 6–9 μ, in clavate forms the wall 1–2 μ thick, thicker above, 2–5 μ, colorless, smooth; uredinio-spores globoid or broadly ellipsoid, small, 13–16 by 15–20 μ; wall colorless, moderately thin, 1.5–2 μ, closely and finely verrucose.

III. Telia hypophyllous, scattered, irregularly roundish, 0.2–0.4 mm. across, reddish-brown, subepidermal, indehiscent, teliospores oblong or prismatic, rounded at both ends, 7–12 by 30–32 μ; wall light-brown, uniformly thin, about 1 μ, smooth.

On *Abies balsamea* (L.) Mill., Pictou, Nova Scotia, June 24, 1910, *W. P. Fraser;* Brule, Wisconsin, June-July, 1913, *E. M. Gilbert;* Fish Creek [Green Bay peninsula], Wisconsin, July 4, 1913, *J. J. Davis;* Alpena, Michigan, June 20, 1914, *C. H. Kauffman;* Walden, Vermont, July 8, 1917, *C. R. Orton.*

On *Abies concolor* Lindl. & Gord., Ouray, Colorado, July 26, 1912, *J. C. Arthur 8504* (Barth. Fungi Columb. *3819*); Palmer Lake, Colorado, July 3, 18, 1913, & July 15, 1916, *E. Bethel.*

On *Salix balsamifera* Barr., Pictou, Nova Scotia (near caeoma on *Abies*), August 27, 1910, II, III, *W. P. Fraser.*

Salix discolor Muhl., Pictou, Nova Scotia, July 17, 1910, II, November (?), 1910 III, *W. P. Fraser* (type, partly used for cultures); Orient, New York, September 7, 1914, II, September 28, 1919, II, *Roy Latham.*

Salix humilis Marsh., Orient, New York, September 19, 1915, II, III, *Roy Latham 647.*

On *Salix monticola* Bebb, Palmer Lake, Colorado, September 6, 1913, II. *E. Bethel.*

On *Salix pedicellaris* Pursh, Solon Springs, Wisconsin, August 13, 1915, II, III, *J. J. Davis.*

On *Salix Scouleriana* Barr., Libby, Montana, October 15, 1911, ii, III, *James R. Weir;* Ouray, Colorado, July 24, 1912, II, *Mrs. J. C. Arthur 4307;* Palmer Lake, Colorado, September 6, 1913, II, iii, *E. Bethel*, September 20, 1913, II, III, *Bartholomew & Bethel 5669.*

On *Salix Wrightii* And., Brazito, New Mexico, November 1, 1915, ii, III, *W. A. Archer 25.*

This is a common and abundant species, extending practically throughout the United States and southern Canada, and probably

southward through Mexico and Central America. It has heretofore passed under the name of *Melampsora arctica*. The type selected for the species is the collection on *Salix discolor* Muhl., made by W. P. Fraser at Pictou, Nova Scotia, November (?), 1910, and partly used for successful cultures in May, 1911, on *Abies balsamea*, which were reported in Mycologia (4: 187–188. July, 1912).

The first aecia of this species seen by the writer were forwarded by Professor Fraser in 1910. Word was returned that they were an undescribed form, probably belonging to *Melampsora arctica* on *Salix*. Telial material on *Salix* was secured by Professor Fraser in the fall, and sown on *Abies balsamea* in May, 1911, with abundant success (*cf.* Mycologia *l.c.*). Representative specimens were sent to the writer, and these now constitute the type material for the new species. A similar culture was made in June, 1912 (*cf.* Mycologia 5: 238. 1913).

An entirely independent set of observations and cultures was made by Mr. E. Bethel in Colorado. He obtained aecia on *Abies concolor* at Palmer Lake, Colorado, July 15, 1916, and on the following morning made sowings in his garden at Denver, on three species of willow. Eighteen days afterward, August 3, an abundance of uredinia was found on two plants, one probably *Salix Bebbiana*, and the other probably *S. Scouleriana*, but on two other equally vigorous plants of *S. amygdaloides* there was no indication of infection. Representative specimens with notes are in the Arthur herbariun.

All the aecial collections known to the writer, with the exception of one uncertain specimen from the state of Washington, are mentioned above, and most of the telial collections. But some forty collections believed to belong here, mostly with uredinia only, are not listed. The unlisted specimens include the hosts: *Salix cordata* Muhl., *S. exigua* Nutt., *S. Fendleriana* And., *S. lasiolepis* Benth., *S. lutea* Nutt., *S. Mackenziana* Barr., *S. Nelsoni* Ball, *S. sitchensis* Sans., *S. taxifolia* H. B. K., as well as the cultivated forms, *S. alba* L., *S. babylonica* L., *S. Caprea* L., and *S. purpurea* L. These collections come from the following states in addition to those mentioned above: Alaska, Arizona, California,

Idaho, Oregon, Washington, West Virginia, Virginia; Alberta, British Columbia; Guatemala.

I am indebted to Mr. Ivar Jorstad, plant pathologist to the government of Norway, for calling my attention to the misapplication of the name *Melampsora arctica*. While in this country in 1919–20 he paid two visits to Purdue University, and made most helpful suggestions regarding the synonymy and limitation of a number of species to appear soon in the North American Flora. He pointed out that no rust was known in Europe corresponding to the American caeoma on *Abies*.

Mr. Jorstad further directed attention to the essential identity of *Melampsora alpina* Juel and *M. arctica* Rostr., as given in the 7th volume of the North American Flora, pp. 99, 100, and as confirmed by his own studies. In Greenland, where Rostrup's material was obtained, various species of *Saxifraga*, on which the aecia are to be looked for, are common, while species of *Abies* are absent. In Europe *M. alpina* Juel has been cultured by means of *Saxifraga* caeoma on *Salix herbacea*, the common American host recorded for *M. arctica*. *M. arctica* is the older name, and the species to which it properly applies is a boreal form with aecia on Saxifragaceae, and entirely distinct from the more southern *M. americana* with aecia on *Abies*.

Pucciniastrum americanum (Farl.) comb. nov.

Pucciniastrum arcticum americanum Farl. Rhodora **10**: 16. 1908.

This species differs from *Pucciniastrum arcticum* (Lagerh.) Tranz., with which it has been united, especially by the narrow, urceolate peridium, which is readily distinguished from the broad, low peridium of *P. arcticum*, even under a low power of the microscope. *P. arcticum* is a boreal species, chiefly known from northern Europe and Alaska. In Alaska it occurs on *Rubus stellatus* Smith and *R. Chamaemorus* L. Outside of Alaska only two American collections are known, one on *R. pubescens* Raf. (*R. triflorus* Richards.), from Grand Manan, New Brunswick, August, 1888, *K. Miyabe*, and one on *R. occidentalis* L., from Algona, Wisconsin, September, 1914, *B. O. Dodge*.

P. americanum is more southern and a much more abundant species. It ranges through the southern part of Canada from

British Columbia to Nova Scotia, and southward to Iowa and West Virginia. It is especially abundant in the northeastern United States on *Rubus strigosus* Michx., and less so on *R. occidentalis* L. It also occurs on *R. pubescens* Raf., and in the northwest on *R. melanolasius* Focke. The aecia for both *Pucciniastrum arcticum* and *P. americanum* are unknown.

Puccinia offuscata sp. nov.

II. Uredinia amphigenous, scattered, round or oval, 0.3–1 mm. long, rather tardily naked, pulverulent, dark cinnamon-brown, ruptured epidermis conspicuous; paraphyses intermixed with the spores, slightly clavate, 5–9 by 29–48 μ, the wall 1 μ thick, colorless, smooth; urediniospores broadly ellipsoid or broadly obovoid, 18–23 by 23–29 μ; wall cinnamon-brown, 1.5–2.5 μ thick, finely and closely echinulate, the pores 3 or 4, equatorial.

III. Telia hypophyllous, few, scattered, round, 0.1–0.3 mm. in diameter, rather tardily naked, compact, dark cinnamon-brown, ruptured epidermis conspicuous; teliospores clavate, 13–18 by 32–53 μ, rounded above, narrowed below, slightly constricted at septum; wall light golden-brown, 1–2 μ thick, slightly thickened at apex, 1–5 μ, smooth; pedicel up to one half length of spore, colorless.

On *Zornia bracteata* (Walt.) Gmel. (*Z. tetraphylla* Michx.), Braidentown, Florida, May 11, 1900, II, *S. M. Tracy 6583*.

On *Zornia diphylla* (L). Pers., Pinar del Rio, Cuba, April 23, 1903, II, iii, *J. A. Shafer 292;* Herradura, Cuba, September 30, 1904, II, iii, *C. F. Baker 2143* (type); same, November 26, 1917, II, *F. S. Earle 822;* Mayagüez, Porto Rico, March 7, 1916, II, *Whetzel & Olive 200;* Barcelonita, Porto Rico, April 6, 1916, II, *Whetzel & Olive 199.*

This species of rust has heretofore passed under the name of *Uredo Zorniae* or *Puccinia Zorniae*, names which properly apply to the Old World species on the same two hosts as listed above. The two species differ noticeably in both urediniospores and teliospores. The Old World species has urediniospores with two pores, or an occasional spore with three pores, and the teliospores are not so elongated, much constricted at septum, with the two cells nearly of the same size and shape, being globoid. An excellent description and an illustration from a photograph are given by McAlpine, Rusts of Australia, page 172, *pl. 10, f. 87.*

The teliospores of *P. offuscata* have been found only in the province of Pinar del Rio, Cuba. The earliest record was brought to light by Mr. Percy Wilson from a collection in the phanerogamic herbarium of the New York Botanical Garden, made by Shafer on a dry plateau, doubtless not far from Herradura. The teliospores, which have not yet been found in abundance, germinate *in situ* upon maturity. The same species occurs in the vicinity of Rio de Janeiro, Brazil (Hedwigia **38**: 257. 1899), and also in in northern Brazil (Hedwigia **43**: 161. 1904).

Puccinia senilis sp. nov.

II. Uredinia hypophyllous, scattered, 0.2–0.4 mm. in diameter, early naked, pulverulent, yellow, ruptured epidermis inconspicuous; urediniospores obovoid or broadly ellipsoid, 15–18 by 19–23 μ; wall light-yellow, 1 μ thick, sparsely echinulate, the pores very inconspicuous, apparently 3 or 4, equatorial.

III. Telia amphigenous, scattered, round, 0.1–0.3 mm. in diameter, early naked, pulverulent, chocolate-brown, ruptured epidermis inconspicuous; teliospores ellipsoid, 18–24 by 27–40 μ, rounded at both ends, somewhat constructed at septum; wall dark chestnut-brown, 1.5 2.5 μ thick, 5–7 μ over the germ-pores, often with a semihyaline cap over apex, coarsely and moderately verrucose; pedicel colorless, up to 50 μ long, tapering downward and roughened below, fragile.

On *Lippia myriocephala* Cham. & Schlecht., Laguna on Lake Amatitlan, Guatemala, January 20, 1906, II, III, *W. A. Kellerman 5451*. Only the one collection is known, of which the corresponding host collection, numbered 5209, was determined by John Donnell Smith. The material is not abundant but the rust appears distinct and unequivocal. If the wall of the teliospores were more evidently laminated, there could be no hesitancy in placing it under the genus *Prospodium*, although pycnia have not been detected. The species seems closely related to *Puccinia peruviana* Sydow, from western South America on *Lippia urticoides*.

Puccinia gulosa H. S. Jackson, sp. nov.

III. Telia caulicolous and petiolicolous, oval or elliptic, gregarious, frequently confluent along somewhat swollen stems and petioles for 1–2 cm., early naked, cinnamon-brown, pulverulent, ruptured epidermis noticeable; teliospores ellipsoid or oblong,

15–18 by 26–35 μ, rounded above and below, strongly constricted at septum; wall cinnamon-brown, 1.5–2 μ thick, with a small subhyaline umbo over the pore of the upper cell, 2.5–3 μ, finely but noticeably verrucose-rugose, best seen when dry; pedicel colorless, short, fragile, largely disappearing.

On *Polemonium pulcherrimum* Hook., Colby Mountains, above Muir Gorge, Yosemite National Park, California, 8500 feet altitude, August 6, 1919, *Mrs. Mary Strong Clemens 24*.

This species appears to be a short-cycle form, although no pycnia or germinating teliospores were found. It is similar to *P. Polemonii* Diet. & Holw., which is known by the type collection from Idaho, 1892, and one collection from southern Indiana, 1919. That species, however, has narrower, smooth spores, with a decidedly thickened apex, 4–6 μ. The sori of the latter are compact, and show abundant germination, while the sori of the new species are pulverulent, and show no germinating spores.

Puccinia proximella (Arth.) comb. nov.

Uredo proximella Arth. Mycologia 7: 324. 1915.

Recently in studying this West Indian rust Dr. E. B. Mains discovered teliospores on the type collection made at Sabana Grande, Porto Rico, March 30, 1913, *F. L. Stevens 318*, and has drawn up the following description:

III. Telia hypophyllous, scattered, rather tardily naked, ruptured epidermis conspicuous; teliospores ellipsoid or oblong, 21–27 by 26–42 μ, rounded above and below, slightly constricted at septum; wall dark chestnut-brown, uniformly thick, 1.5–2 μ, moderately and distinctly verrucose; pedicel colorless.

Puccinia hiascens nom. nov.

Puccinia aucta Arth. & Holway; Arth. Am. Jour. Bot. 5: 475. 1918. Not *P. aucta* Berk. & Müll. 1872.

The recent discovery that the name applied to this Guatemalan rust on *Saurauja* had previously been used for a very different Australian rust necessitates a change in the name.

Puccinia Heterisiae H. S. Jackson, nom. nov.

Puccinia aspera Diet. & Holway; Arth. Bull. Torrey Club 29: 230. 1902. Not *P. aspera* Bon. 1869.

Dasyspora aspera Arth. Résult. Sci. Congr. Bot. Vienne 346. 1906.

Professor Jackson, who has been working upon the group to which this rust belongs, has suggested a change of the name, as the one under which it is now known he finds to be preoccupied. The rust is on *Heterisia Mertensiana* (Bong.) Small (*Saxifraga Mertensiana* Bong., *S. heterantha* Hook.), and beside the type collection from Mt. Adams (Mt. Paddo), Washington, at about 2000 meters altitude, is now known by an ample collection from the vicinity of Grinnell glacier, 1650–1950 meters altitude, Glacier National Park, Montana, July 31, 1919, *Paul C. Standley 16814*.

Uromyces imperfectus nom. nov.

Uredo Bauhiniae Berk. & Curt. Proc. Am. Acad. 4: 126. 1860.
Uromyces Bauhiniae Vesterg. Ark. Bot. Stockh. 4^{15}: 21. 1905.
Not *U. Bauhiniae* P. Henn. 1895.

As the specific name for this species is preoccupied, a new name becomes necessary. Only two collections have been seen by the writer, one being the type collection from Nicaragua, and the other from Moneague, Jamaica, February 24, 1915, *E. W. D. Holway 231*, both showing only uredinia.

Uredo contraria sp. nov.

II. Uredinia hypophyllous, scattered, round, minute, 0.1–0.3 mm. in diameter, early naked, yellow, very pulverulent, ruptured epidermis inconspicuous; urediniospores oblong or obovate-oblong, 20–24 by 27–35 μ; wall colorless, 1.5–2 μ thick, finely and rather sparsely echinulate, the pores obscure.

On *Phacelia tanacetifolia* Benth., Carmel, California, April 15, 1919, *E. W. D. Holway*, July 4, and October 1, 1919, *Mrs, Joseph Clemens*.

This rust, in its gross appearance and even in the microscopic appearance of its spores, resembles species of *Pucciniastrum*, but careful sectioning of the sori shows them to be applanate, and without peridium or paraphyses. The spores are produced in abundance, and due to their bright yellow contents, make a considerable showing of yellow powder on the under side of the leaves. The species occurs among the sand dunes where *Pinus radiata* grows, and along the dusty roadsides of the region. It was watched

for a number of months by Professor Holway, and from January to October by Mrs. Clemens, but no other stage of development could be detected.

Uredo nitidula sp. nov.

II. Uredinia amphigenous, scattered, roundish or oblong, 0.3–0.7 mm. across, rather tardily naked, pulverulent, dark cinnamon-brown, ruptured epidermis conspicuous; urediniospores obovoid or ellipsoid, 18–24 by 24–29 μ; wall cinnamon-brown, 1.5–2 μ thick, moderately echinulate, the pores 2 or 3, equatorial.

On *Alternanthera philoxeroides* Griseb., Cahabon, Guatemala, October 27, 1877, *Von Türckheim.*

This collection is represented by a specimen in the cryptogamic herbarium of the New York Botanical Garden, where it is labelled "*Uredo? paranensis* Penningt." It is, however, noticeably different from the species indicated in having smaller spores with thinner walls.

Uredo laeticolor nom. nov.

Uredo Operculinae Arth. Mycologia **9**: 95. 1917. Not *U. Operculinae* Sydow, Phil. Jour. Sci. **8**: 476. 1913.

My attention has been called to the earlier use of the name which I gave to this convolulaceous rust from the West Indies. The name was used by the Sydows for a Philippine rust on *Operculina turpethum*, which appears from the description to have somewhat smaller and thicker walled spores, more inclined to be globoid, and paler in color.

Aecidium Ixorae sp. nov.

O. Pycnia epiphyllous, scattered unevenly over large discolored areas often 4–8 cm. across, punctiform, prominent, dark-brown, becoming whitish by age, subepidermal, flattened hemispherical, 150–200 μ in diameter, about half as high, with a flat hymenium; ostiolar filaments wanting.

I. Aecia hypophyllous, opposite the pycnia, scattered, deep-seated, cylindric, 0.2–0.3 mm. across; peridium colorless, the margin strongly recurved, lacerate; peridial cells rhombohedric, strongly imbricate, the exposed inner face about 16–19 μ across, in section much prolonged downward on outer side, the inner wall about 3 μ thick, verrucose, the outer wall about 2 μ thick, smooth; aeciospores globoid, small, 16–19 μ in diameter; wall colorless, 1 μ or less thick, finely verrucose, appearing smooth.

On *Ixora ferrea* (Jacq.) Benth. (*Siderodendron triflorum* Vahl), Bahia Honda, Cuba, October 28, 1919, *S. C. Bruner 1133*.

A very distinctive form, and especially remarkable in having hemispherical pycnia with flat hymenia, that are beneath the firm epidermis, opening at first by a minute central pore to discharge the pycniospores, and in all characters similar to pycnia heretofore known only as subcuticular. The large areas over which the original infection seems to spread, producing a brown, deadened appearance on both surfaces of the thick, leathery leaves, make the species an easy one to detect in the field. Mr. Bruner writes that the type locality is in a rather inaccessible district in the mountains, some six miles from the village of Bahia Honad.

Aecidium indecisum sp. nov.

O. Pycnia hypophyllous, scattered over all or large areas of the leaves among the aecia, conspicuous, honey-yellow, subepidermal, in section globoid, 80–110 μ in diameter; ostiolar filaments long.

I. Aecia hypophyllous, scattered from a diffused mycelium, cupulate, 0.3–0.5 mm. in diameter, projecting but slightly above the host tissue; peridium remaining somewhat incurved and covered by the host tissues, the margin erose; peridial cells in section oblong or rhomboidal, 16–26 by 30–40 μ, abutted, or slightly overlapping, the outer wall thick, 8–10 μ, transversely striate, smooth, the inner wall thinner, 3–6 μ, closely and rather finely verrucose; aeciospores ellipsoid or globoid, 16–19 by 21–26 μ; wall colorless, thin, 1–1.5 μ, closely and inconspicuously verrucose.

On *Ranunculus californicus* Benth., Berkeley, California, March 11, 1893 (Sydow, Ured. *900;* Barth. N. Am. Ured. *1303*), *W. C. Blasdale.*

This appears much like *Aecidium Ranunculi* Schw., the name under which it has been distributed, but differs in its much more robust development, the measurements in every way being greater. *A. Ranunculi* Schw. is known to be the aecial form of *Puccinia Eatoniae* Arth. on species of *Sphenopholis*. Both this rust and its telial host are only known from east of the Rocky Mountains. It may be assumed that the California aecia are heteroecious, and belong to some inconspicuous and rather evanescent grass rust, probably not yet reported.

There has probably been but one collection of this form made, although dates on the different packets in herbaria are not uniform. The date on the Sydow distribution is "31.5.1894," but a packet in the herbarium of the New York Botanical Garden, reads "March 31, 1894," so I assume that "5" is a misreading of "3." The Bartholomew distribution gives March 11, 1893. This material was received through Professor E. W. D. Holway, who obtained it from the collector. Possibly there were two collections made in consecutive years, but the appearance of the material does not warrant the assumption. I am using the material distributed by Bartholomew as the type.

Aecidium Mitellae Ellis & Ev., sp. nov.

O. Pycnia not seen.

I. Aecia hypophyllous, in crowded circular groups 2–3 mm. across; peridia cupulate, small; aeciospores globoid, or broadly ellipsoid, 15–18 by 18–26 μ; wall thin, 1 μ, colorless, minutely verrucose.

On *Mitella nuda* L., Shoal Point, Bay of Islands, Newfoundland, *Waghorne.*

The specimen from which this description is drawn is in the cryptogamic herbarium of the New York Botanical Garden, and consists of a single leaf bearing three groups of aecia. The specimen appears to have been sent to Mr. J. B. Ellis by Waghorne, although the collector's name is not written on the packet. The packet bears the doubtful date of "13.7.82," which possibly indicates that the material was secured on July 13, 1882. A note accompanies the specimen, reading, "This seems to be on various leaves and stems of this *Mitella;* I have only one leaf more." Whether this was written by Mr. Waghorne or Mr. Ellis is uncertain. There seems to be no doubt about the identity of the host, or the genuineness of the rust, so that the name given by Mr. Ellis and apparently not heretofore published, should be established. The form appears to be a heteroecious one.

Aecidium subsimulans Arthur & Mains, sp. nov.

O. Pycnia amphigenous, on brownish or reddish spots 2–5 mm. across, noticeable, cinnamon-brown, subepidermal, flattened-

globoid, 95–125 μ broad by 60–95 μ high; ostiolar filaments up to 125 μ long.

I. Aecia hypophyllous, crowded in spots with the pycnia, cylindric, 0.2–0.3 mm. wide, 0.5–1 mm. high; peridium white, the margin somewhat erect, erose; peridial cells rhomboidal, 19–26 by 32–45 μ, somewhat overlapping, the outer wall thick, 9–13 μ, transversely striate, smooth, the inner wall 4–6 μ thick, closely and rather coarsely verrucose; aeciospores globoid or ellipsoid, 19–23 by 23–29 μ; wall colorless, 1.5–2.5 μ thick, very closely and finely verrucose.

On *Salvia candicans* Mart. & Gall., hills about Tehuacan, State of Puebla, Mexico, 1895, *C. G. Pringle.*

On *Salvia Lemmoni* A. Gray, Carr Peak, Huachuca Mountains, Arizona, August 25, 1910, *L. N. Goodding 856* (type).

On *Salvia* sp., Sierra de Pachuca, State of Hidalgo, Mexico, July 20, 1905, *Rose, Painter & Rose 8792.*

This species somewhat resembles the aecia of *Puccinia caulicola* Tr. & Gall., as well as the Mexican *Aecidium zonatum* Sacc., but the walls both of the spores and of the peridial cells are much thicker. Dr. Mains, who has made a special study of the *Salvia* rusts, has joined me in deciding upon the status of this species.

Aecidium Betheli sp. nov.

O. Pycnia not seen.

I. Aecia hypophyllous, subepidermal, in small and crowded groups 1–3 mm. across, on a hemispherical, hypertrophied substratum, cupulate, small, 0.1–0.2 mm. in diameter; peridium low, erect, the margin erose; peridial cells readily falling apart, rhomboidal, 13–18 by 19–23 μ, strongly overlapping, the outer wall 7–9 μ thick, transversely striate, smooth, the inner wall 1 μ, evenly and noticeably verrucose; aeciospores globoid, small, 13–18 by 16–18 μ; wall colorless, thin, 1 μ or less, very finely and evenly verrucose.

On *Jussiaea californica* (S. Wats.) Jepson, Long Beach, California, August 15, 1916 (type), August 24, 1918, *E. Bethel.*

Found in abundance associated with *Puccinia canaliculata* (Schw.) Lagerh., on *Cyperus esculentus*, but probably not genetically connected, as neither the relationship of the host nor the structure of the aecia agrees with those of the known aecial stage for that species. The species is dedicated to the discoverer, who

is one of the most active and resourceful observers of the Uredinales among American botanists, and who has explored the Rocky Mountain and Pacific coast rust flora with unparalleled thoroughness.

Aecidium arctoum sp. nov.

O. Pycnia epiphyllous and to a less extent hypophyllous among the aecia, numerous, rather inconspicuous, small, subepidermal, in section globoid, 128–160 μ in diameter; ostiolar filaments prominent, up to 80 μ long.

I. Aecia hypophyllous, subepidermal, diffused on slightly paler spots 3–7 mm. across, cupulate, very small, 0.1–0.2 mm. in diameter; peridium delicate, erect or somewhat recurved, the margin erose or fimbriate; peridial cells rhomboidal, 16–19 by 28–32 μ, somewhat overlapping, the outer wall 1–1.5 μ thick, smooth, the inner wall 3–6 μ thick, moderately verrucose; aeciospores globoid, or some of them oblong, 21–26 by 23–29 μ; wall colorless, thin, 1–1.5 μ, minutely verrucose.

On *Elaeagnus angustifolia* L., Kulm, North Dakota, June 24, 1919, *J. F. Brenckle 1235*.

The form described here as a new species was found in considerable abundance on a hedge of the Eurasian oleaster in the town of Kulm. Dr. Brenckle, who submits the material, could find no rusted grass or sedge in the vicinity that seemed at all likely to serve as the alternate host, although it is undoubtedly a heteroecious species. The supposition that the rust could have been imported with the hedge plants can be dismissed as highly improbable, even aside from the fact that no aecial form on this group of hosts is known in the region where the host is native.

The spores are very much smaller than those of *Aecidium Allenii* Clint., on *Elaeagnus argentea* from North Dakota, as well as those of *A. Elaeagni* Diet. and *A. minoense* Sydow from Japan. There is a Japanese form on *Elaeagnus glabra* with spores of nearly the same size, but it has larger and firmer aecia, and other characteristics which distinguish it. In spite of the appearance of this form on an exotic shrub under conditions of cultivation, it seems most likely to be a native rust that has found a congenial host in this foreign plant.

Aecidium renatum sp. nov.

O. Pycnia epiphyllous, inconspicuous, subepidermal.

I. Aecia hypophyllous, subepidermal, thickly covering the surface of the leaf, short cylindric, 0.2–0.4 mm. in diameter; peridium erect, erose; peridial cells rhomboidal, 16–19 by 26–32 μ, strongly overlapping, the outer wall 3–5 μ thick, smooth, the inner wall 6–9 μ, prominently verrucose; aeciospores globoid, 19–23 by 21–24 μ; wall colorless, thin, 1 μ, closely and finely verrucose.

On *Polygala longa* Blake, Organ Mountains, New Mexico, August 29, 1894, *E. O. Wooton*.

This is a species similar in character and appearance to *Aecidium polygalinum* Peck on *Polygala Senega* from the northern United States, but has a more vigorous development, with larger aecia and aeciospores.

Aecidium arcularium sp. nov.

O. Pycnia epiphyllous, gregarious, minutely punctiform, inconspicuous, subepidermal, in section globoid or depressed-globoid, 100–130 μ broad by 90–100 μ high; ostiolar filaments up to 45 μ long.

I. Aecia hypophyllous and caulicolous, usually densely crowded in groups 4–10 mm. across; peridium cylindric, the margin erect, erose or deeply lacerate; peridial cells ellipsoid or oblong, angular, 21–29 by 27–40 μ, the cells overlapping, the outer wall 5–10 μ thick, transversely striate, smooth, the inner wall 2–5 μ thick, finely verrucose; aeciospores globoid or ellipsoid, 18–23 by 22–29 μ; wall colorless or pale cinnamon-brown, 1–1.5 μ thick, finely verrucose.

On *Coleosanthus grandiflorus* (Hook.) Kuntze (*Brickellia grandiflora* Nutt.), Beulah, New Mexico, 1889, *T. D. A. Cockerell;* Cloudcroft, New Mexico, September 16, 1903, *E. W. D. Holway;* Upper Miller Canyon, Huachuca Mountains, Arizona, August 14, 1909, Boulder Canyon, Colorado, August, 1914, *E. Bethel;* Ute Park, Colfax County, New Mexico, August 20, 1916, *Paul C. Standley 13383;* Grousemont, Platte Canyon, Colorado, July, 1918, *Mrs. Emily Arthur* (type); Idaho Springs, Colorado, August 7, 1919, *J. M. Bates 6987*.

A conspicuous species, usually occurring in abundance within limited area. It is sometimes associated with uredinia or telia of *Puccinia subdecora* Syd. & Holw., which for a time was supposed to be genetically connected with it. No suggestion has yet been made regarding the alternate stages.

Aecidium Liabi sp. nov.

O. Pycnia epiphyllous, somewhat loosely grouped on discolored areas, inconspicuous, dark-brown, subepidermal, ellipsoid, about 95 by 128 μ; ostiolar filaments short, about 45 μ.

I. Aecia hypophyllous, in groups up to 8 mm. in diameter, cupulate, 0.3–0.8 mm. in diameter; peridium pale-yellow, fragile; peridial cells rhomboidal, 19–23 by 35–55 μ, considerably overlapping, the outer wall 2–5 μ thick, smooth, the inner wall thicker, 5–7 μ, closely tuberculate-verrucose; aeciospores angularly globoid, 21–26 by 26–31 μ; wall colorless, 1.5–2.5 μ thick, closely and distinctly verrucose.

On *Liabum* sp., Jalapa, State of Veracruz, Mexico, September 2–4, 1910, *A. S. Hitchcock*.

Aecidium Batesii sp. nov.

O. Pycnia mostly epiphyllous, in groups 1–3 mm. in diameter, noticeable, subepidermal, chestnut- or chocolate-brown, flattened-globoid, 125–160 μ broad by 90–115 μ high; ostiolar filaments up to 95 μ long.

I. Aecia amphigenous, loosely grouped upon brownish spots 4–8 mm. across, cupulate, 0.5–0.8 mm. in diameter; peridium yellowish, the margin remaining for a time incurved, covered more or less by the epidermis, finally becoming recurved, lacerate; peridial cells oblong, 15–19 by 32–35 μ, slightly overlapping or abutted, the outer wall rather thick, 6–10 μ, transversely striate, smooth, the inner wall thinner, 3–4 μ, closely and finely verrucose; aeciospores angularly globoid, 19–23 by 24–27 μ; wall colorless, 1–1.5 μ thick, very closely and finely verrucose.

On *Rudbeckia hirta* L., Callaway, Nebraska, May 31, 1901, *J. M. Bates 1814½*.

This rust has something the appearance of the aecia of *Puccinia Stipae*, having large spores, in peridia that are partly covered for a time by the epidermis. It is named in honor of its discoverer, who has for many years been indefatigable in making the rust flora of Nebraska known, and whose field observations and collections from all parts of the state have been freely placed at the service of students of the Uredinales.

Aecidium Mesadeniae sp. nov.

O. Pycnia epiphyllous, few, crowded in small groups, 1–2 mm. across, inconspicuous, dark-brown, subepidermal, flattened-glo-

boid, 95–125 μ broad by 50–65 μ high; ostiolar filaments up to 40 μ long.

I. Aecia usually hypophyllous, crowded in groups 2–6 mm. across, cupulate, small, 0.1–0.3 mm. in diameter; peridium pale-yellow, the margin recurved, lacerate; peridial cells rhomboidal, 14–18 by 24–29 μ, overlapping, the outer wall 7–9 μ thick, transversely striate, smooth, the inner wall 2–3 μ thick, closely and rather finely verrucose; aeciospores globoid or ellipsoid, small, 12–16 by 15–19 μ; wall colorless, thin, 1 μ or less, closely and finely verrucose.

On *Mesadenia atriplicifolia* (L.) Raf. (*Cacalia atriplicifolia* L.), Manhattan, Kansas, May, 1886, *W. A. Kellerman* (Rab.-Wint.-Paz. Fungi Eur. *3833a*), same, June, 1886 (Ellis & Ev. N. Am. Fungi *1811*), Valley Park, Missouri, May, 1887 (*L. H. Pammel?*).

On *Mesadenia reniformis* (Muhl.) Raf. (*Cacalia reniformis* Muhl.), Somers, Wisconsin, June 3, 1894, *J. J. Davis* (type).

The type collection of this species was found in abundance in a small area where *Uromyces minimus* Davis, on *Muhlenbergia sylvatica*, also occurred, and at the time was thought might be its aecial stage (Bot. Gaz. **19**: 415. 1894; Bull. Lab. Nat. Hist. Univ. Iowa **5**: 315. 1902). That assumption has not been disproven but seems less probable now than at first.

Aecidium praecipuum sp. nov.

O. Pycnia amphigenous, in small groups about 2 mm. across, noticeable, pale-yellow becoming dark-brown, subepidermal, flattened-globoid, 110–130 μ broad by 80–95 μ high; ostiolar filaments up to 60 μ long.

I. Aecia hypophyllous, crowded on spots 2–10 mm. across, short cylindric, 0.3–0.5 mm. in diameter; peridium pale-yellow, the margin erect, erose; peridial cells irregularly oblong, 20–23 by 32–40 μ, considerably overlapping by a long projection of the outer wall, the outer wall thick, 9–11 μ, the inner wall thinner, 4–4.5 μ, closely and noticeably verrucose; aeciospores angularly globoid or ellipsoid, 16–19 by 19–26 μ; wall colorless, thick, 2.5–3.5 μ, very closely and inconspicuously verrucose.

On *Senecio praecox* DC., Mt. Montezuma, Sierra de Guadelupe, State of Mexico, Mexico, July 8, 1905, *Rose, Painter & Rose 8028;* Sierre de Pachuca, State of Hidalgo, Mexico, July 20, 1905, *Rose, Painter & Rose 8791* (type).

PURDUE UNIVERSITY,
LAFAYETTE, INDIANA

INDEX TO AMERICAN BOTANICAL LITERATURE

1916–1920

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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BULLETIN

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TORREY BOTANICAL CLUB

NOVEMBER, 1920

Studies in the genus Lupinus—V. The Sparsiflori

CHARLES PIPER SMITH

(WITH FOURTEEN TEXT FIGURES)

INTRODUCTION

The Californian annuals of the subgenus *Lupinus* have long been recognized as separating into two divisions, the verticillate-flowered forms and those with flowers not in verticils. As already shown by me (Bull. Torrey Club **46**: 390), this classification holds good in the subgenus *Platycarpos*, if one exception is provided for. It likewise may be applied to the annuals and biennials of North America in general, north of Panama, but breaks down in the *Micranthi*, a large assemblage of variations usually with real verticils. Serious study of the material examined prompts recognition of at least five groups, only one of which will be treated in this paper. These groups will include the so-called biennials of Texas and adjacent Mexico. My classification contrasting these groups will be presented in a subsequent paper.

The following published names appertain to plants here assigned to the *Sparsiflori:*

L. hirsutissimus Benth. Trans. Hort. Soc. II. **1**: 141. 1835.

L. leptophyllus Benth. *Ibid.* II. **1**: 141. 1835.

L. truncatus Nutt.; Hooker & Arnott, Bot. Beechey Voy. 336. 1840.

L. sparsiflorus Benth. Pl. Hartw. 303. 1848.

L. concinnus arizonicus Wats. Proc. Am. Acad. 8: 537. 1873.

L. arizonicus Wats. *Ibid.* **12**: 250. 1876.

[The BULLETIN for October (**47**: 441–486) was issued October 29, 1920.]

L. citrinus Kell. Proc. Cal. Acad. Sci. I. **2**: 192. 1877.
L. Pondii Greene, Pittonia **1**: 288. 1899.
L. deflexus Congdon, Muhlenbergia **1**: 38. 1904.
L. Benthami Heller, *Ibid.* **2**: 61. 1905.
L. subhirsutus Davidson, Bull. So. Cal. Acad. Sci. **18**: 80. 1919.

L. arizonicus Wats. was proposed to replace *L. concinnus* var. *arizonicus* Wats., and *L. Benthami* Heller is a proper substitute for *L. leptophyllus* Benth., since the latter was published five years later than the Mexican *L. leptophyllus* Schl. & Cham. Instead of ten, however, I recognize only six species, one of these being extremely variable and exhibiting marked variation in several directions.

The home of these plants is mainly in southern California, from Monterey Bay and El Dorado County to northern Lower California; but certain variations of *L. sparsiflorus* extend southward to the tip of Lower California, including some of its adjacent islands, and others spread eastward over the Mexican Plateau region of Arizona, etc.

The principal diagnostic characters of this group are: annuals with non-verticillate flowers, racemes 2–30 cm. long, longer than their supporting peduncles; keel petals ciliate below near the claw and commonly also ciliate above.

Key to the species of the Sparsiflori

Largest leaflets 15–20 mm. wide; plants conspicuously hispid with stinging hairs mainly 3–5 mm. long. — 1. *L. hirsutissimus.*
Largest leaflets 2–12 mm. wide; plants not obviously hispid, the the hairs not over 2 mm. long.
  Flowers obviously ascending after anthesis. — 2. *L. sparsiflorus.*
  Flowers spreading or drooping after anthesis.
    Leaflets truncate at apex, entire, notched, or three-toothed.
      Leaflets cuneate-oblong, petioles terete. — 2. *L. sparsiflorus.*
      Leaflets linear, petioles usually flattened. — 3. *L. truncatus.*
    Leaflets angled at apex, mostly acute.
      Matured pods ascending; petals blue and purple. — 4. *L. Benthami.*
      Pods deflexed; petals not blue.
        Plants 1–2 dm. tall; petals orange or golden; pods two-to four-seeded. — 5. *L. citrinus.*
        Plants 2–4 dm. tall; petals white or pinkish; pods five-to eight-seeded. — 6. *L. deflexus.*

1. LUPINUS HIRSUTISSIMUS Benth. Trans. Hort. Soc. II. 1: 141. 1835. [FIG. 53.]

Stout, 2–5 dm. tall, the very stiff hairs 3–5 mm. long and nettle-like; leaflets five to eight, broadly cuneate-obovate, 15–20 mm. wide, 20–50 mm. long; racemes 15–25 cm., flowers about 14 mm. long, spreading, pedicels 3–4 mm. long; calyx with stiff spreading hairs, the upper lip about 6 mm. long, bifid, the lobes slender, acuminate, 3 mm. wide, lower lip entire and acuminate or three-toothed, 8–9 mm. long, 4 mm. wide; petals dark or light purple, banner nearly orbicular, including the claw about 14 x 14 mm., wings about 14 x 8 mm., keel stout, straight, ciliate at the free edges below, naked above; pods 20–30 mm. long, stiffly hirsute like the rest of the plant, ovules about seven; seeds about 3 mm. long, thin, pale and obscurely marked or densely marbled with dark brown.

This is, perhaps, the most sharply contrasted annual lupine of southern California, its long stinging yellow trichomes setting it

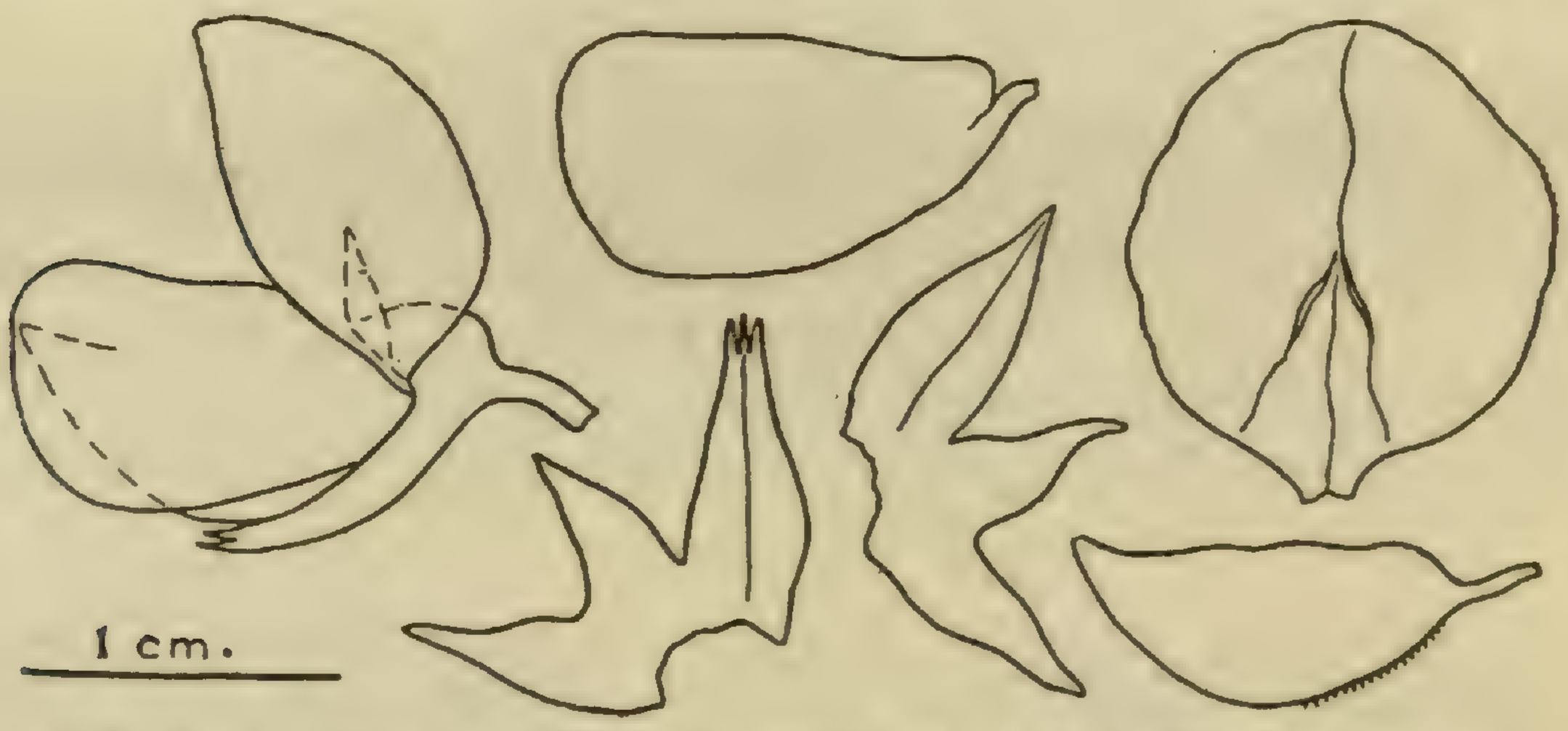

FIG. 53. LUPINUS HIRSUTISSIMUS Benth. *E. A. McGregor 703* (CPS).

apart as unique. Once known, it should never be confused with any other species, not even the stiffest-haired forms of *L. sparsiflorus*. The original description, though certainly abbreviated, leaves no doubt as to the identity of the species. I quote a few clauses, as follows:

> L annuus, undique pilis longis rigidis patentibus hirsutissimus . . . foliolis obovatis mucronulatis . . . flowers reddish-purple.

CALIFORNIA. Los Angeles County: Claremont, March, 1897, *H. P. Chandler* (UC); same, May, 1909, *C. F. Baker 5358* (B, G, NY, US, CPS); Glendora, May, 1902, *G. B. Grant 727* (B);

Los Angeles, *Miss E. D. Palmer* (UC); Pasadena, May, 1886, *Julia A. Meeker* (B); same, March, 1893, *A. J. McClatchie* (NY); Pomona, April, 1902, *E. Braunton 224* (US); San Clemente Island, June, 1903, *B. Trask 255* (NY, US); same, May, 1916, *K. Brandegee* (UC); Santa Catalina Island, Avalon, May, 1898, *B. Trask* (US); Santa Catalina Island, March, 1901, *B. Trask* (NY); Santa Monica Forest, March, 1897, *J. H. Barber 57* (B, G, UC); Santa Monica, Rustic Canyon, Feb., 1900, *C. A. Colmore* (UC). Monterey County: Little Sur River, May, 1901, *J. B. Davy 7372* (UC); Santa Lucia Mountains, San Migueleta ranch, May, 1897, *A. Eastwood* (G); Santa Lucia Mountains, Willow Creek, March, 1898, *R. A. Plaskett 64* (G, NY, UC). Riverside County: Elsinor, April, 1892, *A. J. McClatchie* (NY). San Benito County: San Juan, May, 1903, *A. E. D. Elmer 4732* (NY, US). San Bernardino County: Cajon Hills, April, 1891, *G. W. Dunn* (RM); Mentone, April, 1898, *J. B. Leiberg 3288* (US); Redlands, May, 1906, *L. A. Greata* (B); San Bernardino Mountains, May, 1880, *G. R. Vasey 94* (US); same, April, 1906, *S. B. Parish 5665* (RM); San Bernardino foothills, May, 1885, *S. B. & W. F. Parish 144* (UC, US); same, April, 1888, *S. B. Parish* (UC); San Bernardino, May, 1894, *S. B. Parish* (US); San Bernardino hills, May, 1898, *S. B. Parish* (NY); near San Bernardino, March, 1901, *S. B. Parish 4658* (NY, US); same, April, 1903, *S. B. Parish 5185* (B); San Bernardino valley, May, 1909, *S. B. Parish 7086* (UC); Waterman Canyon, June, 1894, *S. B. Parish 3493* (US). San Diego County: Fallbrook, Moro Hill, *L. R. Abrams 3337* (G, NY, US); Jacumba, April, 1889, *C. R. Orcutt* (US 21034, right-hand specimen); Julian, Laguna Mountains, June, 1918, *E. A. McGregor 703* (CPS); La Jolla, Howard Canyon, March, 1914, *F. S. & E. S. Clements 152* (G); San Diego, May, 1862, *J. G. Cooper 539* (US); same, March, 1885, *C. R. Orcutt* (T); same, March, 1892, *O. W. Knight 2325* (G); same, March, 1901, *K. C. Brandegee* (UC); same, May, 1906, *T. S. Brandegee* (B, NY); San Pasqual, May, 1852, *G. Thurber 610* (G, NY, T); San Ysabel, April, 1893, *H. W. Henshaw 130* (US); Witch Creek, May, 1894, *R. D. Alderson* (UC). San Luis Obispo County: San Luis Mountain, Feb., 1886, *Mrs. R. W. Summers*

(G, NY, UC); San Luis Obispo, spring, 1905, *J. E. Roadhouse 34* (UC). Santa Barbara County: Cuyama River, May, 1896, *A. Eastwood* (G); San Rafael Mountains, June, 1887, *H. C. Ford* (G); Santa Barbara, March, 1861, *W. H. Brewer 316, 340* (G, US); Santa Cruz Island, April, 1888, *T. S. Brandegee* (UC); Santa Inez Mountains, March, 1828 (UC). Santa Cruz County: near Santa Cruz, *C. L. Anderson* (UC). County not given: Santa Ana River, April, 1880, *Parish Brothers* (B); 1876, *C. C. Parry & J. G. Lemmon 63* (G, T); *Dr. Coulter 373* (T); April, 1884, *Mrs. R. W. Summers* (US).

LOWER CALIFORNIA. Cariso Creek, April, 1893, *T. S. Brandegee* (UC); Guadalupe Mountains, May, 1883, *C. R. Orcutt 880* (NY); Laguna to Tia Juana River, June, 1894, *E. A. Mearns, International Boundary Commission 3505* (NY); San Telmo, April, 1886, *C. R.Orcutt* (UC).

2*a*. LUPINUS SPARSIFLORUS Bent. Pl. Hartw. 303. 1848. [FIG. 54.]

Lupinus subhirsutus Davidson, Proc. So. Calif. Acad. Sci. **18**: 80. 1919.

This is a composite species exhibiting several pronounced variations, which, in their extremes, readily lend themselves to a scheme of classification. Numerous intermediates occur, however, and comparative study shows the advisibility of recognizing a series of varieties here, rather than several new species not at all equal in rank to *L. hirsutissimus*, *L. Benthami*, *L. truncatus*., etc.

From Bentham's description I quote the following:

> Pili patentes cum aliis appressis mixta . . . Flores iis *L. nani* subsimilis, omnes alterni v. rarius hinc inde approximati.

My conception of the species, both *sensu lato* and *sensu stricto*, is indicated by the following diagnosis, the italics emphasizing the characters not shared by the typical form.

Stems slender or *stouter and more or less fistulous*, usually branched, appressed-pubescent and usually more or less villous, the spreading hairs some 1–2 mm. long, either soft or quite stiff; leaflets five to nine, linear, oblanceolate, *cuneate*, *cuneate-oblong*, or *elliptic*, angled, *truncate*, or *notched* at the apex, somewhat hairy or almost glabrous above, usually villous below, petioles terete: flowers 8–13 mm. long, promptly and conspicuously be-

coming suberect as the petals wither and the ovaries enlarge; petals bright blue or *pale purplish*, banner suborbicular with poorly defined claw or *somewhat longer than wide and abruptly contracted into a well-defined claw*, keel petals short ciliate, rarely naked, at the free edges below, naked or sparsely ciliate above; pods ascending, about six-ovuled; seeds some 2–3 mm. long, angled, dotted or marbled on a pale ground.

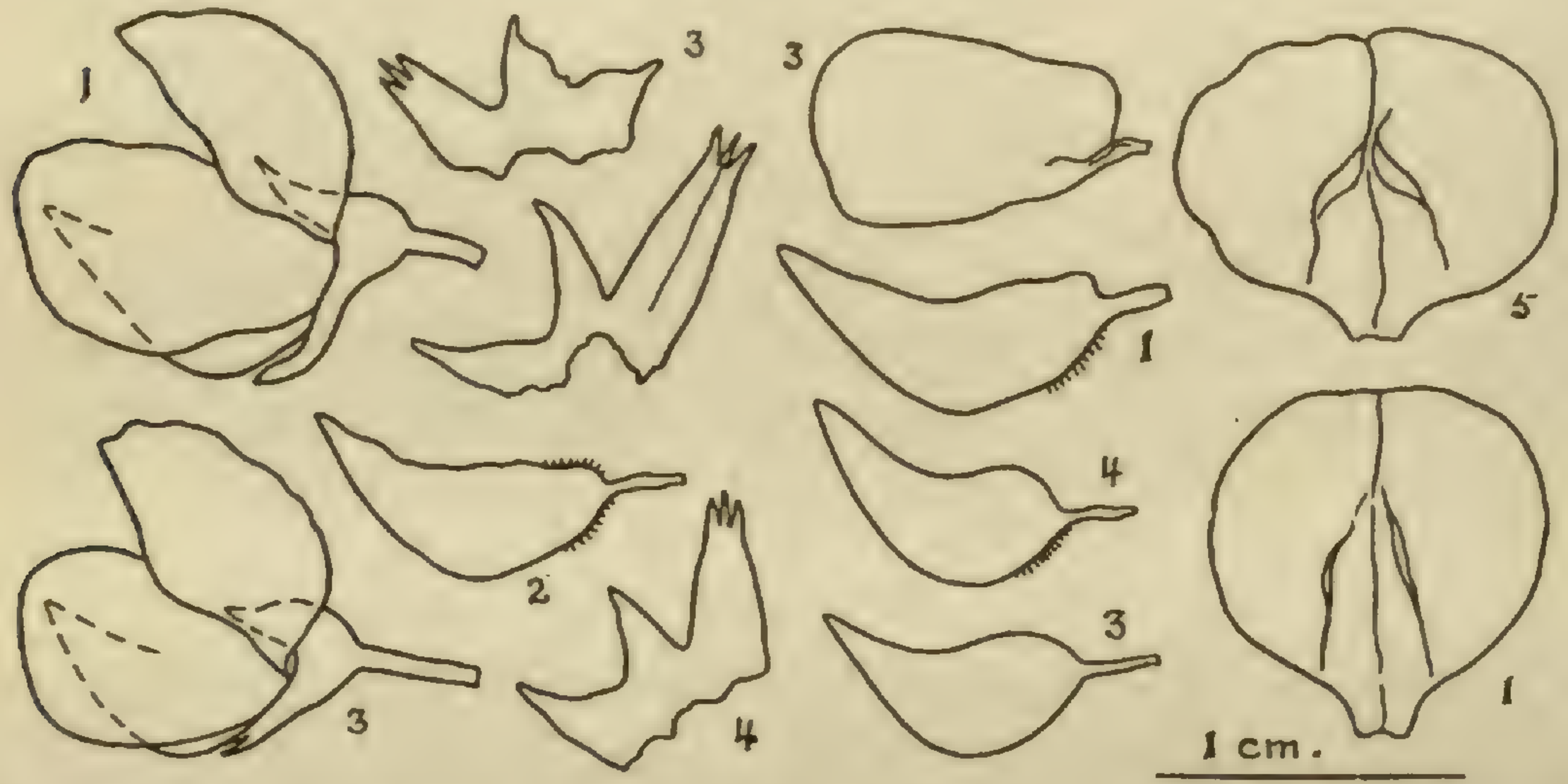

FIG. 54. LUPINUS SPARSIFLORUS Benth. 1. *C. F. Baker 5357* (CPS); 2. *J. Grinnell* (US 614572); 3. *F. S. Daggert* (G. L. Moxley); 4. *H. M. Hall 5759* (UC); 5. *I. Tidestrom 867* (US).

After much deliberation, I am still unable to accept Dr. Davidson's *L. subhirsutus* as of even varietal rank. That the keel, as stated by him, is really non-ciliate, has been verified by my dissection of flowers from a type-duplicate specimen in the collection of Mr. Geo. L. Moxley, of Los Angeles. However, the keel is normally ciliate in Dr. Hall's specimens (UC) from Palm Springs, the type locality of *L. subhirsutus*. That *L. sparsiflorus* is quite variable at Palm Springs is shown by the fact that, before Dr. Davidson's description was published, I had listed certain specimens from there as var. *arizonicus*, and others as var. *barbatulus*. The distinction as to nodose and non-nodose hairs I I have not yet been able to appreciate.

As indicated further by key, the varieties here recognized are distinguished by stem and leaflet characters, the often evident differences in amount and length of the spreading hairs being rejected as quite unsatisfactory for diagnostic use within the limits of this species. Each of these varieties could in turn be subdivided

into obviously villous forms and appressed-pubescent or glabrate forms; but too many specimens are intermediate in this respect and too few are really typical of the extremes.

Specimens assigned to the species, *sensu stricto*, are:

LOWER CALIFORNIA. Punta Gorda, April, 1892, *T. S. Brandegee* (G, UC, US).

CALIFORNIA. Los Angeles County: Antelope Valley, May, 1896, *J. B. Davy 2323* (UC); Azusa, San Gabriel Wash, March, 1906, *J. Grinnell* (US); Chatsworth Park, San Fernando Mountains, April, 1901, *L. R. Abrams 1344* (G); Claremont, April, 1904, *C. F. Baker 4103* (UC); same, May, 1909, *C. F. Baker 5357* (CPS); Elycian Hills, near Occidental College,. Feb., 1903, *E. Braunton* (UC); Garvanza, April, 1901, *G. B. Grant* (US); Garvanza, April, 1902, *H. M. Hall 2939* (B); Llano Verde foothills, May, 1896, *J. B. Davy 2325* (UC); Los Angeles, March, 1880, *J. F. James* (US); same, 1884, *J. C. Nevin 22a* (G, UC); same, May, 1903, *E. D. Palmer* (UC); Newhall, Oct., 1884, *J. C. Nevin 22b* (G); Pasadena, March, 1880, *J. F. James* (US); same, March, 1893, *A. J. McClatchie* (US); same, Feb., 1903, *G. B. Grant* (B); same, May, 1904, *G. B. Grant* (RM, UC); Pomona, April, 1897, *J. H. Barber 141* (G, UC); San Pasqual, May, 1852, *G. Thurber* (G); Saugus, May, 1889, *K. Brandegree* (UC); Sierra Madre, Mt. Wilson trail, June, 1914, *C. P. Smith 2877* (CPS). Orange County: San Juan, April, 1903, *L. R. Abrams 3277* (G, UC, US). Riverside County: Coahuilla foothills, April, 1902, *H. M. Hall 2903* (UC); Corona, April, 1915, *C. N. Collins & J. H. Kempton 11* (US); Cottonwood Pass, May, 1905, *H. M. Hall 5999* (B, UC); Elsinore, April, 1892, *A. J. McClatchie* (NY); Midlands, April, 1903, *H. M. Hall 3846* (G); Palm Springs (Agua Caliente), April, 1896, *S. B. Parish 4080* (NY); Palm Springs, April, 1919, *F. S. Daggert* (flowers from G. L. Moxley's type-duplicate of Davidson's *Lupinus subhirstus*); same, April, 1905, *H. M. Hall 5759* (UC); Riverside, April, 1902, *H. M. Hall 2939* (B, NY, RM, UC, US); same, April, 1903, *Charlotte M. Wilder* (UC); San Jacinto, 1890, *Mrs. Gregory* (UC); Winchester, April, 1897, *H. M. Hall* (UC). San Bernardino County: Cajon Pass, April, 1902, *H. M. Hall 3007* (UC); Colton, April, 1882, *M. E. Jones 3333* (NY, RM, US); Fort Mojave, Feb., 1861, *J. G. Cooper* (UC); Mojave Desert, bordering hills, May,

1882, *C. G. Pringle* (G, T, US); Redlands, April, 1897, *Mrs. A. P. Maynard* (UC); San Bernardino, May, 1880, *G. R. Vasey 102* (US); same, May, 1886, *S. B. & W. F. Parish 946* (G, NY); same, April, 1888, and May, 1893, *S. B. Parish* (UC); same, April, 1901, *S. B. Parish* (NY); same, April, 1903, *S. B. Parish 5195* (B); same, April, 1906, *S. B. Parish 5578* (RM); San Gorgonio Pass, April, 1898, *J. B. Leiberg 3235* (US). San Diego County: Colorado Desert, April, 1889, and April, 1890, *C. R. Orcutt* (US); same, April, 1905, *T. S. Brandegee* (US); Jacumba, April, 1889, *C. R. Orcutt* (US); Sweet-water Valley, May, 1888, *G. C. Deane* (G); Witch Creek, *R. D. Alderson* (UC). Ventura County: Ojai Valley, April, 1896, *F. W. Hubby 35* (UC.).

NEVADA. Clark County: Mica Springs, April, 1894, *M. E. Jones 5064p* (NY, UC, US).

ARIZONA. Maricopa County: Valley Hassayampa, 1876, *E. Palmer 581* (UC). Pima County: Redington to Tanque Verde, March-April, 1903, *D. Griffiths 3781* (US); Santa Catalina Mountains, April, 1908, *J. N. Rose 11809* (US); Santa Rita Forest, March-April, 1903, *D. Griffiths 3800* (US); Tucson, 1905, *Desert Botanical Laboratory* (US); Tucson to Steam Pump, March-April, 1903, *D. Griffiths 3627* (US); Tucson Mountains, March-April, 1903, *D. Griffiths 3482* (US); same, April, 1892, *J. W. Toumey* (US 211805). Pinal County: Dudleyville, March-April, 1903, *D. Griffith* 3715 (US). Santa Cruz County: Calabasas, April, 1908, *I. Tidestrom 867*, (US). County not determined: 1876, *E. Palmer 581* (US 20990); Saginaw Mine road, March, 1901, *D. Griffiths 2493* (NY); Willow Spring Mountain, March-April, 1903, *D. Griffiths 3649* (US).

Key to the varieties of Lupinus sparsiflorus

Leaflets truncate or rounded at apex, entire, notched emarginate, or three-toothed.
  Plants branched about the middle; racemes lax, 6–15 cm. long. — *2f.* var. *inopinatus.*
  Plants branched at or near the base; racemes compact, 2–8 cm. long. — *2g.* var. *Pondii.*
Leaflets angled at apex.
  Largest leaflets 6–12 mm. wide; stems usually stout, 4–10 mm. thick and fistulose or succulent; racemes 8–30 cm. long, petals pale lilac or violet.
    Leaflets mostly six to nine, broadest near the apex. — *2d.* var. *barbatulus.*

Leaflets mostly five (four to six), broadest near the middle. — *2e.* var. *insignilus.*

Largest leaflets 2–4 mm. wide.

Stems stout and fistulose; petals pale lilac or purplish. — *2c.* var. *selosissimus.*

Stems slender, 3–4 mm. thick, hardly succulent or fistulose; racemes 6–15 cm. long, petals usually bright blue.

Flowers 8–10 mm. long. — *2b.* var *arizonicus.*

Flowers 11–13 mm. long. — *2a.* typical *sparsiflorus.*

2b. **Lupinus sparsiflorus arizonicus** (Wats.) comb. nov. [Fig. 55.]

Lupinus concinnus arizonicus Wats. Proc. Am. Acad. 8: 537. 1873.

Lupinus arizonicus Wats. *Ibid.* 12: 250. 1876.

Differs from *L. sparsiflorus* Benth. only in reduced stature and in size of flowers, which are from 8–10 mm. long; pubescence as in the typical plant, limited to short subappressed hairs or with few to abundant longer spreading hairs.

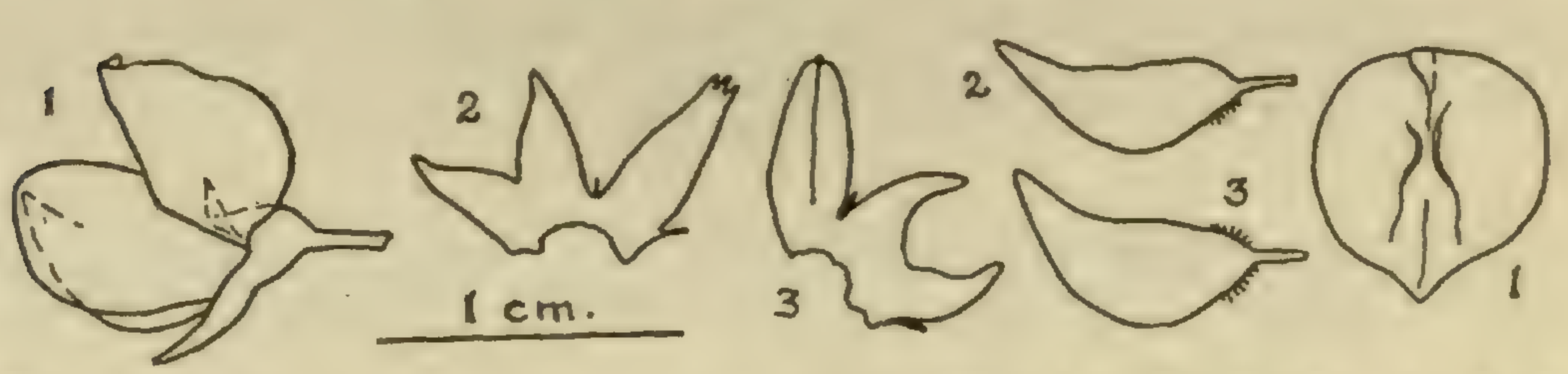

FIG. 55. LUPINUS SPARSIFLORUS ARIZONICUS (Wats.) C. P. Smith. 1. *M. E. Jones 5051* (US); 2. *M. Tuck* (US 348958); 3. *Rose, Standley & Russell 15090* (US).

Through intermediates its relationship to both the typical form and var. *barbatulus* is evident.

ARIZONA. Cochise County: Camp Lowell mesas, April, 1881, *C. G. Pringle* (NY, US); Benson, April, 1905, *T. E. Wilcox* (US). Greenlee County: Clifton, April, 1879, *A. Davidson 133* (G); San Francisco Mountains, near Clifton, April, 1881, *H. H. Rusby* (G). Maricopa County: Phoenix, March, 1897, *R. E. Kunze* (NY). Mohave County: near Kingman, June, 1893, *N. C. Wilson* (UC); mesa near Mellen, Feb., 1910, *J. Grinnell* (UC); Mica Spring, March, 1894, *M. E. Jones 4053* (RM, US), *5045g, 5051* (US); Yucca, May, 1884, *M. E. Jones 3885* (NY, T, US). Pima County: Loasa to Lavare, *via* Baboquivari,

D. Griffith 3601 (US); Santa Catalina Mountains, April, 1894, *J. W. Toumey 6* (G); same, April, 1895, *J. W. Toumey* (UC, NY); Sabina Canyon, near Tucson, April, 1896, *Myrtle Zuck* (NY, US); Santa Rita Range Reserve, May, 1912, *E. O. Wooton* (US); Tucson Mountains, April, 1892, *J. W. Toumey 571* (B, NY, UC, US); Tucson, spring, 1907, *F. E. Lloyd* (G); same, 1876, *E. Palmer 582* (US). Yavapai County: Walnut Grove, April, 1876, *E. Palmer 86* (G, US). County not given: Agua Verde Creek, April, 1914, *J. A. Harris C14153* (US); Beaver Dam, 1877, *E. Palmer 85* (G); Diamond Creek Canyon, April, 1893, *N. C. Wilson* (UC); 1884, *J. G. Lemmon 39* (G).

NEVADA. Clark County: El Dorado Canyon, April, 1919, *I. Tidestrom 8758* (CPS, US).

CALIFORNIA. Riverside County: Chuchawalla Springs, April, 1905, *H. M. Hall 5891* (B, UC); Cottonwood Springs, May, 1916, *S. B. Parish 10851* (UC); Mecca, May, 1916, *S. B. Parish 10862* (G); Palm Springs, April, 1919, *A. J. Perkins* (CPS); Riverside Mountains, Colorado River, March, 1910, *J. Grinnell* (UC). San Bernardino County: Mojave River, May, 1884, *E. Palmer 96* (G); the Needles, May, 1884, *M. E. Jones* (NY); San Bernardino, 1880, *J. G. Lemmon 35* (G).

SONORA. Magdalena, April, 1910, *J. N. Rose, P. C. Standley & P. G. Russell 15090* (US).

2*c*. **Lupinus sparsiflorus setosissimus** var. nov. [FIG. 56.]

A *L. sparsifloro* typico differt caule crasso fistulosoque, foliolis lanceolati-linearis longissimis: caule subhirsuto erecto; racemo 8–20 cm. longo, floribus 10 mm. longis, pedicellis 3–5 mm. longis; calyce bracteolato, bracteolis filiformis, 2 mm. longis, labio superiore bifido, inferiore tridentato; vexillo 10 mm. longo, 9 mm. lato, carina prope ungue subter ciliata.

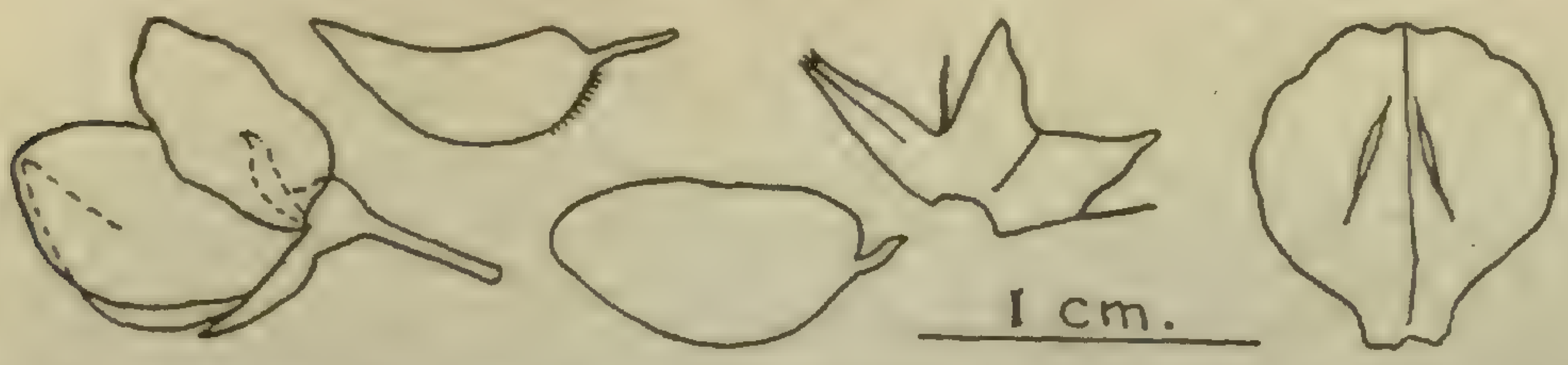

FIG. 56. LUPINUS SPARSIFLORUS SETOSISSIMUS C. P. Smith. *Dr. Streets* (US 21077).

Simple, 2–4 dm. tall, well-provided with stiff spreading hairs, stout and fistulose; basal leaves largest, the cauline few and poorly developed, petioles up to 8 cm. long, leaflets lance-linear, 3–4 cm. long, 3–4 mm. wide; raceme 8–12 cm. long in flower, elongating in fruit, flowers 10 mm. long, bracts subpersistent, setaceous, 4–8 mm. long, pedicels 3–5 mm. long, densely appressed-pubescent; calyx bracteolate, the bractlets 2 mm. long, filiform, upper lip bifid, 4 mm. long, lower three-toothed, 5 mm. long; petals pale lilac or purplish, banner 10 mm. long, 9 mm. wide, wings 9 x 5 mm., keel ciliate below near claw, the point upturned; pods and seeds unknown.

LOWER CALIFORNIA. 1875, *Dr. Streets, U. S. Navy* (TYPE, US 21077).

A rather pronounced variation, not matched by any other specimens seen by me and unfortunately not well labelled. The name is not my own selection, but was applied to the sheet by someone whose handwriting I was unable to get identified. It evidently was suggested by the conspicuous stiff hairs.

2*d*. **Lupinus sparsiflorus barbatulus** Thornber, var. nov. [FIG. 57.]

A *L. sparsifloro* typico differt caule plus minusve fistuloso, foliolis 7–9, oblanceolatis, maximis 6–12 mm. latis; caule erecto; racemo 10–30 cm. longo, floribus 10–11 mm. longis; calyce plurimum ebracteolato, labio superiore bifido, inferiore tridentato; vexillo prope 10 x 10 mm., carina ad basin subter ciliata.

Erect, 3–5 dm. tall, fistulose or succulent, simple or with a few branches, appressed-pubescent and with few or many stiffish spreading hairs; leaflets seven to nine, oblanceolate, glabrous or subglabrous above, 2–3 cm. long, 6–12 mm. wide, broadest near the angled apex; peduncles 6–8 cm. long, racemes 10–15 cm. or more long, flowers scattered, 10–11 mm. long, bracts semi-persistent, filiform, stiff-hairy, exceeding the buds, pedicels 3–4 mm. long; calyx usually ebracteolate, upper lip bifid, 4–5 mm. long, the lobes 1–2 mm. wide at base, lower lip three-toothed, 4–7 mm. ong, about 2 mm. wide; petals pale lilac or purplish, banner orbicular, about 10 x 10 mm., wings 9–10 mm. long, 5–6 mm. wide, keel ciliate on free edges below near claw, nearly straight or with the point decidedly upturned.

ARIZONA. County not given: valley of the Colorado, March, 1876, *E. Palmer 88* (TYPE, US 20666; type-duplicates, T, UC 82181).

CALIFORNIA. Riverside County: Painted Canyon, northeast of Mecca, March, 1917, *E. A. McGregor 725* (CPS); Palm Springs (Agua Caliente), April, 1896, *S. B. Parish 4080* (UC); Palm

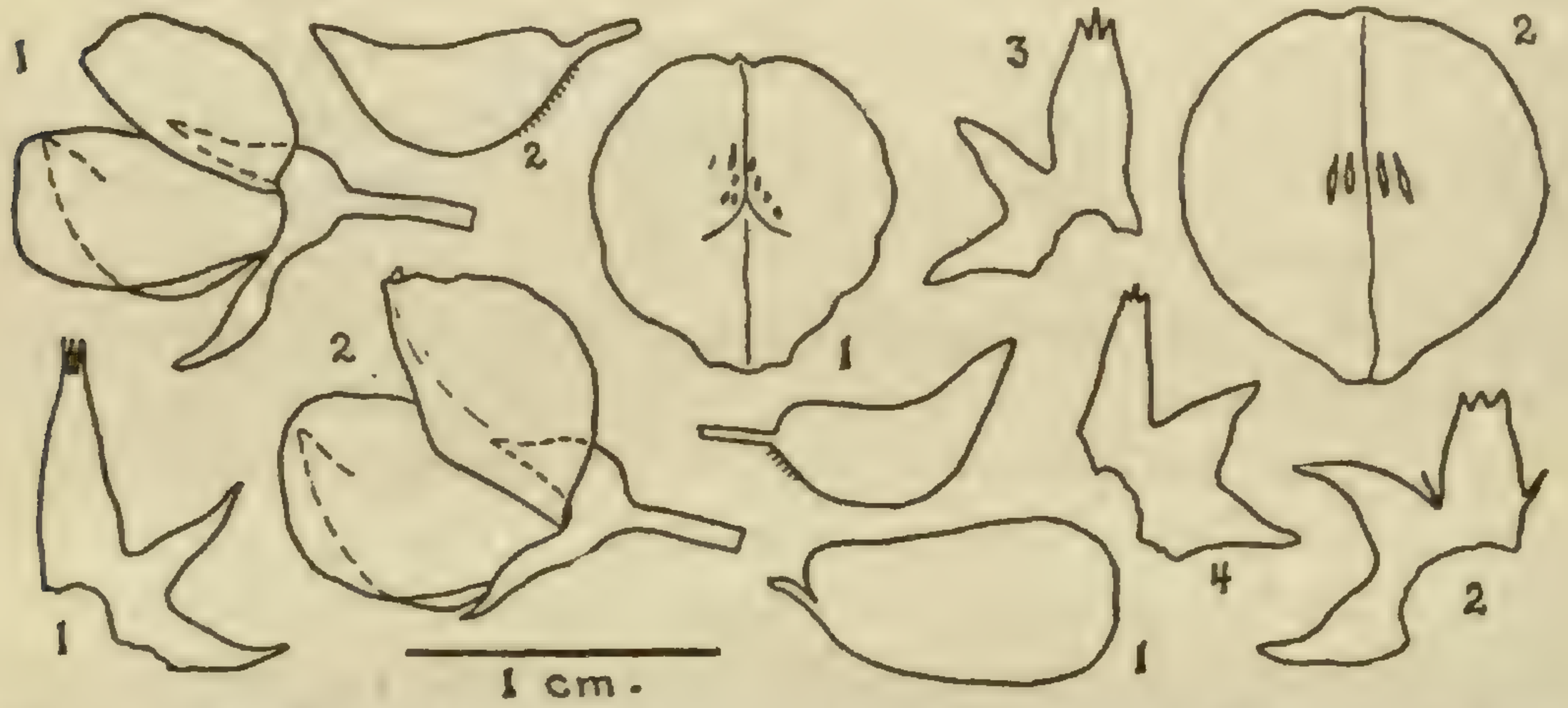

FIG. 57. LUPINUS SPARSIFLORUS BARBATULUS Thornber. 1. *E. Palmer 88* (US) 2. *E. A. McGregor 725* (CPS); 3. *E. Palmer 586* (US); 4. *E. Palmer 595* (US)

Springs, April, 1905, *H. M. Hall 5759* (B); same, April, 1906, *G. B. Grant 6783* (UC); same, May, 1906, *G. B. Grant 723* (B); western borders of Colorado Desert, April, 1907, *S. B. Parish 6152* (B). San Bernardino County: the Needles, March, 1915, *S. B. Parish* (UC). San Diego County: Colorado Desert, April, 1905, *T. S. Brandegee* (US 735442); San Filipe Creek, April, 1901, *T. S. Brandegee* (UC).

LOWER CALIFORNIA. Cabo San Lucas, Nov., 1902, *T. S. Brandegee* (UC); Lagoon Head, March, 1889, *E. Palmer, 797* (G, T, UC); La Palmia, March, 1892, *T. S. Brandegee* (G); Los Angeles Bay, 1887, *E. Palmer 586* (US 20937), *595* (G, US); Palmilla, Jan.-March, 1901, *C. A. Purpus 343* (UC); Punta Gorda, April, 1892, *T. S. Brandegee 117* (G, US); San Ignacio, April, 1889, *T. S. Brandegee* (UC); San Jose del Cabo, Nov., 1898, *T. S. Brandegee* (UC); same, Nov., 1902, *T. S. Brandegee* (UC); Sierra de la Laguna, Jan., 1890, *T. S. Brandegee 117* (UC).

Some time ago, while at the National Herbarium, J. J. Thornber picked out E. Palmer's "Arizona" and "Los Angeles Bay" specimens (US), cited above, and annotated the sheets to indicate

a new species, designating the "Arizona" specimen as the type and applying the name here accepted and accredited to him. I at first readily accepted Professor Thornber's separation as a good species; but as my studies continued and my conception of *L. sparsiflorus, sensu lato*, developed, I was forced to acknowledge the very close relationship of this new form to the typical *L. sparsiflorus*. Intermediates connect it with at least three of the varieties here recognized.

Barbatulus is Latin, diminutive of *barbatus*, "bearded."

2*e*. **Lupinus sparsiflorus insignitus** var. nov. [FIG. 58.]

A var. *barbatulo* differt foliolis plerumque 5 solum, ellipticis, ad medium latissimis: planta subglabra vel superne brevi-villosa; racemo 7–15 mm. longo, floribus 12 mm. longis; calyce ebracteolato, labio superiore bifido, inferiore tridentato; vexillo 11 mm. longo, 10 mm. lato, carina prope ungue subter ciliata.

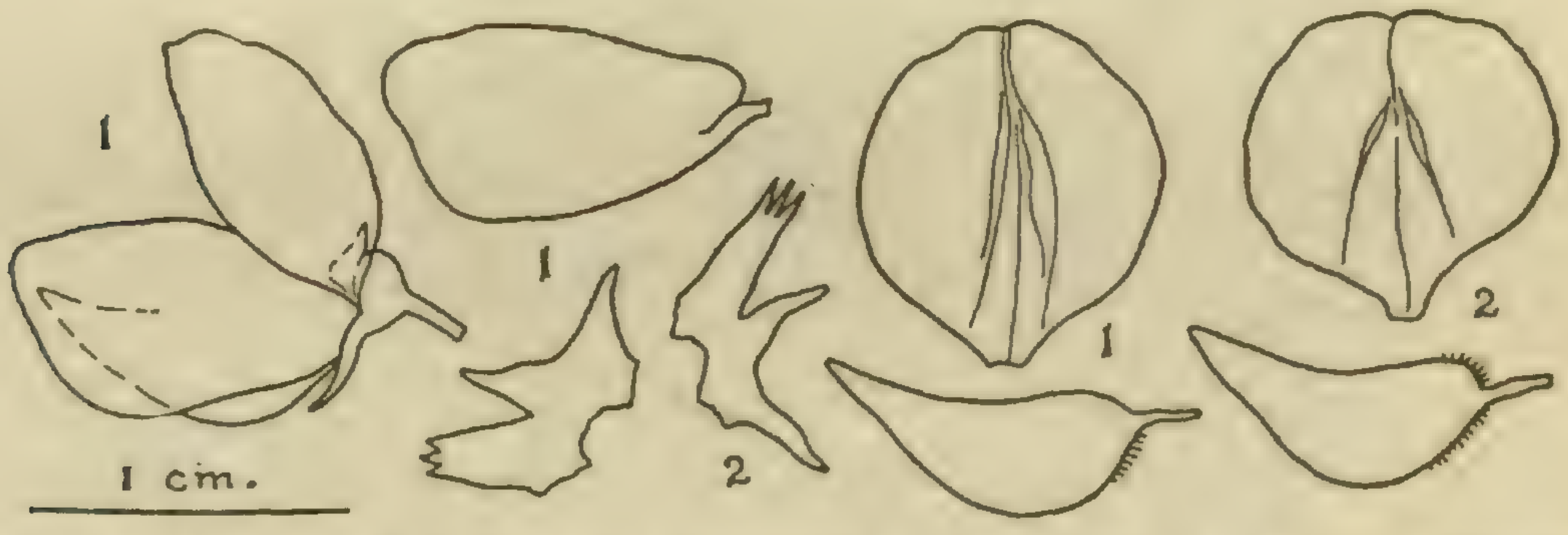

FIG. 58. LUPINUS SPARSIFLORUS INSIGNITUS C. P. Smith. 1. *T. S. Brandegee* (UC 198527); 2. *C. Grabendorffer* (UC 198314).

Very similar to var. *barbatulus* but with the leaflets usually five only (four to six) and broadest near the middle, the pubescence scant and appressed or plentiful and short-spreading in the upper parts: pods ascending, 15 mm. long, 4 mm. wide, five- to six-seeded; seeds about 2 x 1.7 mm., lateral aspect marbled with olive or brown on a light tan ground.

LOWER CALIFORNIA. Santa Margarita Island, March, 1889, *T. S. Brandegee* (TYPE, UC 198527); San Jose del Cabo, 1898, *Carlos Grabendorffer* (UC 198314).

2*f*. **Lupinus sparsiflorus inopinatus** var. nov. [FIG. 59.]

A *L. sparsifloro* typico differt foliolis apice truncatis emarginatis vel minute tridentatis; caule ramoso prope medium; racemo 7–15

cm. longo, floribus prope 12 mm. longis, pedicellis 3 mm. longis; calyce ebracteolato, labio superiore bifido, inferiore tridentato; vexillo plurimum contracto, ungue prope 10 mm. longo, 8 mm. lato, carina plurimum recta prope ungue ciliata.

Slender, branched about the middle, with some spreading hairs, 3–5 dm. tall; leaflets linear-oblanceolate, rounded or truncate at apex, entire, notched, emarginate, or minutely three-toothed; peduncles short, racemes 6–15 cm. long, flowers about 12 mm. long, pedicels about 3 mm., scattered; calyx ebracteolate, upper lip bifid, some 4 mm. long, lower lip three-toothed, 5–6 mm. long; petals seemingly purplish, banner rather abruptly narrowed into a distinct claw, about 10 mm. long and 8 mm. wide, wings 10 x 6 mm., keel 10 mm. long, straight, ciliate below and more or less above near the claw: pods and seeds not seen.

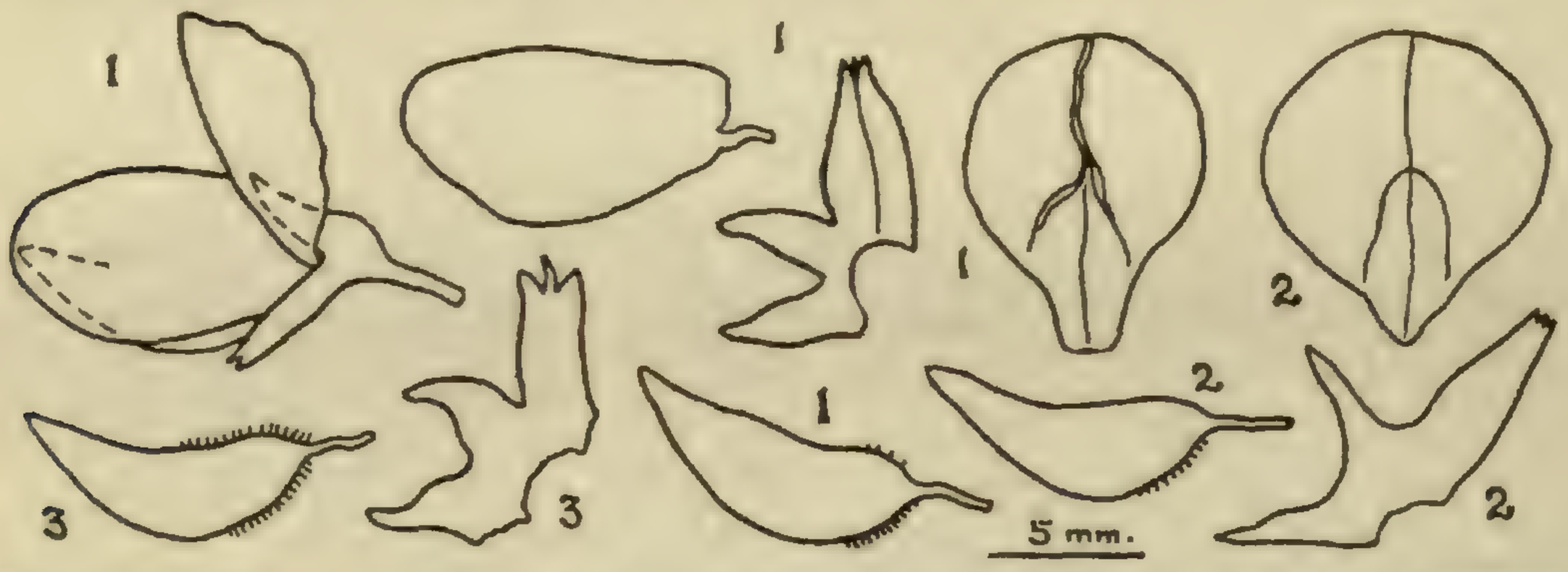

FIG. 59. LUPINUS SPARSIFLORUS INOPINATUS C. P. Smith. 1. *T. S. Brandegee* (UC 444311); 2. *H. M. Hall 3011* (UC); 3. *H. M. Hall 4946* (UC).

CALIFORNIA. Riverside County: Riverside, Fairmount Park, May, 1904, *H. M. Hall 4946* (B, UC). San Bernardino County: Cajon Pass, April, 1902, *H. M. Hall 3011* (UC). San Diego County: San Diego, April, 1903, *T. S. Brandegee*, C. F. Baker's distribution 3411 (TYPE, US 444311; type-duplicates, B, G, NY, RM, UC); same, April, 1905, *K. Brandegee* (UC 198479, in part).

LOWER CALIFORNIA. Arroyo Calmalti, Jan.-March, 1898, *C. A. Purpus 106* (UC); Burro Canyon, April, 1893, *T. S. Brandegee* (UC); hills, April, 1882, *E. Palmer 25* (T); San Gregorio, Feb., 1889, *T. S. Brandegee* (UC); San Quentin Bay, Feb., 1889, *E. Palmer 807* (T); San Sebastean, April, 1889, *T. S. Brandegee* (UC).

The type collection is labelled, "*L. gracilis* Agardh, det. E. L. G." The type sheet is corrected to "*L. sparsiflorus*" by

"L. R. A." and was in the *L. Pondii* cover when first noticed by me. It is likely to be mistaken for *L. truncatus* Benth.

Inopinatus is Latin, used here in the sense of "unexpected."

2*g*. **Lupinus sparsiflorus Pondii** (Greene) comb. nov. [FIG. 60.]

Lupinus Pondii Greene, Pittonia 1: 288. 1899.

Stems branched from the base, 1–3 dm. tall, slender, spreading hairs few to very numerous and stiff; leaflets cuneate-oblong, truncate or notched at the apex, the largest 10–12 mm. long, 2–2.5 mm. wide near apex; peduncles very short, the racemes nearly sessile, 2–8 cm. long, rather densely flowered, flowers 10–12 mm. long, pedicels about 4 mm. long; calyx usually ebracteolate,

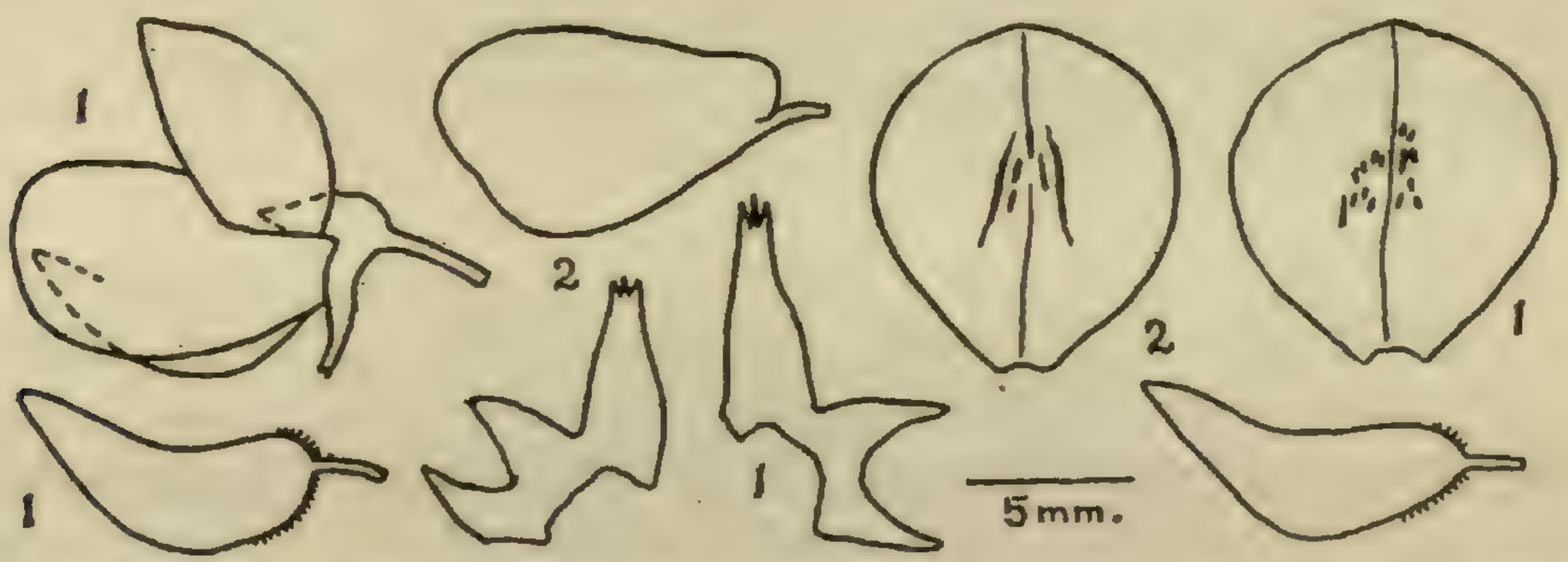

FIG. 60. LUPINUS SPARSIFLORUS PONDII (Greene) C. P. Smith. 1. *A. W. Anthony 284* (US 669752); 2. *J. N. Rose 16157* (US).

upper lip bifid, about 4 mm. long, lower lip three-toothed, 5–7 mm. long; petals probably purplish when fresh, banner suborbicular, about 10 x 10 mm., wings about 10 x 6 mm., keel 9–10 mm. long, 3 mm. wide, the point somewhat upturned, the free edges ciliate below and more or less also above near claw; pods 12–14 mm. long, ovules four or five, seeds about 2 mm. long, smooth, dotted and marbled.

LOWER CALIFORNIA. Aliso, May, 1893, *T. S. Brandegee* (UC); Cedros Island, March-June, 1897, *A. W. Anthony 284* (G, RM, UC, US); same, April, 1897, *T. S. Brandegee* (UC); same, March, 1889, *E. Palmer 721* (G, T, US); same, March, 1911, *J. N. Rose 16157* (NY, US), *16221* (US); El Campo Aleman, April, 1889, *T. S. Brandegee* (UC); El Rosario, 1889, *T. S. Brandegee* (UC); Ensenada, 1889, *T. S. Brandegee* (UC); Las Palmas, April, 1893, *T. S. Brandegee* (UC); Los Angeles Bay Mountains, 1887, *E. Palmer 586* (G); San Bartolomei Bay, March, 1889, *Lieut. Pond* (UC, scrap of TYPE); San Enrique, 1889, *T. S. Brandegee* (UC);

San Felipe, Feb., 1901, *C. Grabendorffer* (UC); San Martin Island, March, 1897, *T. S. Brandegee* (UC); San Quentin, 1889, *E. Palmer 708* (G); San Telmo, May, 1890, *T. S. Brandegee* (UC); San Tomas, April, 1886, *C. R. Orcutt* (NY, UC); Temecala, March, 1882, *M. E. Jones* (G); Tia Juana, April, 1882, *C. R. Orcutt* (UC); locality not given, 1876, *E. Palmer 96* (NY).

CALIFORNIA. San Diego County: Coyote Canyon, Colorado Desert, April, 1902, *H. M. Hall 2821* (UC); Desella, April, 1903, *T. S. Brandegee* (UC).

3*a*. LUPINUS TRUNCATUS Nutt.; Hooker & Arnott, Bot. Beechey Voy. 336. 1840. [FIG. 61.]

Branched, 3–6 dm. tall, appressed-pubescent or practically glabrous; petioles usually flattened, sometimes widely margined, leaflets linear, five to seven, truncate, emarginate or two- to three-toothed at the apex, 20–40 mm. long, 2–3 mm. wide; racemes 6–15 cm. long, very lax and few-flowered; flowers spreading or somewhat drooping after anthesis, 10–12 mm. long, pedicels 2–3 mm. long, bracts usually persistent, lanceolate, 2–3 mm. long; calyx commonly ebracteolate, upper lip bifid, 2–2.5 mm. long, lower lip entire and acute or minutely three-toothed, 4 mm. long; petals more or less dark purple, banner about 10 mm. long, 9 mm.

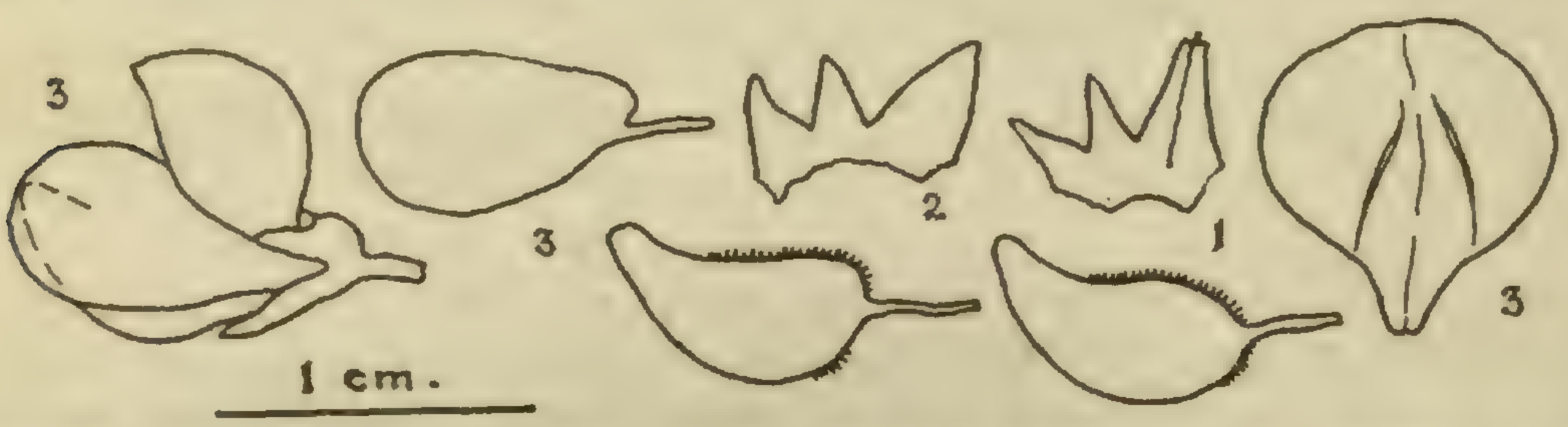

FIG. 61. LUPINUS TRUNCATUS Nutt. 1. *O. W. Knight 6989* (G); 2. *C. P. Smith 2855* (CPS); 3. *C. P. Smith 1446* (CPS).

wide, abruptly contracted into an evident claw, wings about 8 x 5 mm., keel some 8 mm. long, the short stout blunt point upturned, the free edges below more or less ciliate, and densely ciliate above from near the base of the point to near the claw; pods more or less spreading, about 30 mm. long and 5–6 mm. wide, with spreading hairs 1–2 mm. long, ovules six or seven; seeds rhomboid, plump, about 3 x 2.5 mm. in side-view, pale flesh-color with obscure markings of a darker tint, or densely marbled with dark brown.

This is a well defined species. Though superficially resembling *L. sparsiflorus inopinatus*, the two can be easily distinguished

from each other. *L. truncatus* has the pubescence scant and appressed, the petioles flattened, the flowers spreading or subdrooping after anthesis, and the keel densely ciliate above; while the other has some spreading pubescence, normal petioles, flowers suberect soon after anthesis, and the keel naked or nearly so above. San Diego is the type locality of both.

CALIFORNIA. Kern County: Fort Mojave, 1860–61, *J. G. Cooper* (US). Los Angeles County: Antelope Valley, Ells, May, 1896, *J. B. Davy 2606* (UC); Azuza, San Gabriel Wash, March, 1906, *J. Grinnell* (US); Claremont, April, 1904, *C. F. Baker 4191, 4192* (UC); same, April, 1909, *C. F. Baker 5302* (NY, US); Los Angeles, 1880, *J. C. Nevin* (G); same, June, 1904, *Los Angeles High School pupils* (UC); same, Feb., 1920, *F. E. Burlew* (CPS); Pasadena, May, 1904, *G. B. Grant* (UC); San Clemente Island, June, 1903, *B. Trask 257* (NY, US); Santa Catalina Island, May, 1897, *B. Trask* (US); same, May, 1899, *B. Trask* (NY); same, June, 1908, *H. M. Hall 8287* (UC); same, May, 1916, *K. Brandegee* (UC); Santa Monica, May, 1885, *A. Gray* (G); Santa Monica Mountains, April, 1901, *L. R. Abrams 1299* (NY); Sierra Madre, June, 1914, *C. P. Smith 2855* (CPS); Soldiers Home, March, 1897, *J. H. Barber 295* (UC); open grounds and hillsides, May, 1891, *H. E. Hasse* (US); locality not given, April, 1901, *G. B. Grant 3959* (US). Monterey County: Burros, April, 1912, *I. J. Condit* (UC); Monterey, April, 1900, *A. Eastwood* (G); Pacific Grove, June, 1893, *I. Tidestrom* (UC); same, May, 1901, *Mrs. Wright* (UC); same, April, 1903, *A. A. Heller 6637* (G, NY, UC, US); same, May, 1907, *C. P. Smith 1334* (CPS); same, June, 1908, *C. P. Smith 1446* (CPS). Riverside County: Elsinore, March, 1892, *A. J. McClatchie* (NY); Menifee, 1893, *M. A. King* (UC); Moorpark, April, 1912, *E. O. Wooton* (US); Mount Ruleidoux, April, 1913, *R. L. Piemeisel 3436* (US). San Bernardino County: Mentone, April, 1898, *J. B. Leiberg 3292* (US); San Bernardino, May, 1880, *G. R. Vasey 98* (US); same, April, 1881, *W. R. Wright 232* (G); same, March, 1901, *S. B. Parish 4655* (NY) and *4656* (US); San Bernardino foothills, May, 1885, *S. B. & W. F. Parish 69* (UC, US); same, April, 1888, *S. B. & W. F. Parish* (UC); same, May, 1898, *S. B. Parish* (NY); San Bernardino Mountains, Waterman Canyon, June, 1894, *S. B. Parish 3494* (US); San

Bernardino Valley mesas, April, 1908, *S. B. Parish 6928* (UC). San Diego County: Coahuilla foothills, April, 1902, *H. M. Hall 2898* (G, UC, US); Colorado Desert, *A. F. Schott* (US); Dulzura, 1903, *Mr. Valentine* (UC); Fallbrook hills, April, 1903, *L. R, Abrams 3313* (G, NY, US); La Jolla, Rose Canyon, March, 1914, *F. E. & E. S. Clements 151* (G); Lakeside, May, 1889, *T. S. Brandegee* (NY, UC); Lemon Grove road, May, 1904, *H. P. Chandler 5285* (NY); Ocean Beach, May, 1902, *T. S. Brandegee,* Baker's distribution 1602 (G, NY, UC, US); San Diego, May, 1852, *G. Thurber* (G, NY, T); same, March, 1850, *C. C. Parry* (T); same, March, 1892, *O. W. Knight* (G); same, 1904, *T. S. Brandegee* (US); same, May, 1905, *K. Brandegee* (UC); same, April, 1916, *M. F. Spencer 99* (US); San Diego, North Island, May, 1911, *K. Brandegee* (UC); San Ysabel, April, 1893, *H. W. Henshaw 102* (T, US); Sweetwater Valley, April, 1883, and May, 1888, *G. C. Deane* G); Tighes Ranch, 1875, *E. Palmer 53* (G); Witch Creek, April, 1894, *R. D. Alderson.* San Luis Obispo County: Arroyo Grande, April, 1895, *Alice King* (UC); Edno sand dunes, May, 1905, *J. E. Roadhouse 352* (UC); Santa Lucia. Mountains, rocky ravines, March, 1883, *Mrs. R. W. Summers* (G, US); San Luis Mountain, March, 1883, *Rev. R. W. Summers 165* (UC); same, April, 1886, *Mrs. R. W. Summers* (NY); locality not given, April, 1892, *L. Jared* (UC). Santa Barbara County. Alamo Creek, May, 1896, *A. Eastwood* (G); Santa Inez Mountains, April, 1861, *W. H. Brewer 341* (US); Dos Pueblos, Santa Inez, *W. H. Brewer 345* (G); Dos Pueblos, near Gaviote Pass, *W. H. Brewer 385* (G, US); Santa Barbara, May, 1902, *A. D. E. Elmer 4156* (US); Santa Cruz Island, April, 1888, *T. S. Brandegee* (UC). Ventura County: Ojai and vicinity, April, 1866, *S. F. Peckham* (US); Ojai Valley, April, 1896, *F. W. Hubby* (UC), specimens without data, *Douglas, Wallace & Coulter* (G).

LOWER CALIFORNIA. Hills, April, 1882, *C. G. Pringle* (T, US); Nachoguero Valley, June, 1894, *E. A. Mearns,* International Boundary Commission, No. 3496 (US); San Pedro Martin, May, 1893, *T. S. Brandegee* (UC); San Quentin Bay, Jan., 1889, *E. Palmer 636* (G, T, US); Tecabe, July, 1884, *C. R. Orcutt 1096* (G); Todos Santos Island, March, 1897, *T. S. Brandegee* (UC).

3*b*. **Lupinus truncatus Burlewi** var. nov. [FIG. 62.]

A *L. truncato* typico differt floribus minoribus, labio inferiore breviore tridentato 2–3 mm. longo, petalis pallidis, vexillo 8 mm. longo 6 mm. lato, carina subviride recta, 6–7 mm. longa; fructus non vidi.

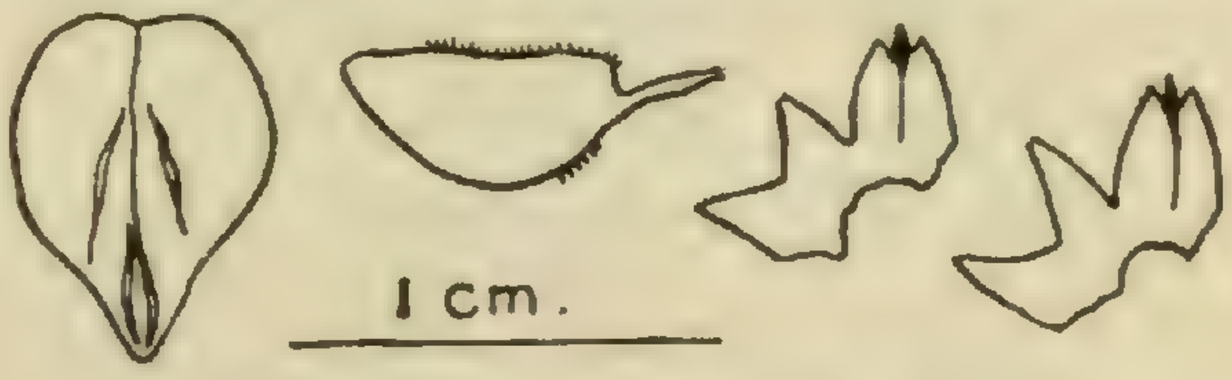

FIG. 62. LUPINUS TRUNCATUS BURLEWI C. P. Smith. *F. E. Burlew* (CPS).

This is a small- and pale-flowered variation, specimens of which have been recently forwarded to me by Mr. Geo. L. Moxley, of Los Angeles. Calyx bright green, lower lip distinctly three-toothed, petals almost devoid of purple, banner 8 x 6 mm., keel 6–7 mm. long, the point not upturned, noticeably greenish; fruit and seeds not seen.

CALIFORNIA. Los Angeles County: rolling hills, Los Angeles, Jan., 1920, *F. E. Burlew* (TYPE, CPS).

4*a*. LUPINUS BENTHAMI Heller, Muhlenbergia 2: 61. 1905. [FIG. 63.]

Lupinus leptophyllus Benth. Trans. Hort. Soc. II, 1: 141. 1835. Not *Lupinus leptophyllus* Schl. & Cham. Linnaea 5: 589. 1830.

Slender, 3–6 dm. tall, villous with spreading hairs about 1.5–2 mm. long; leaflets filiform, 20–50 mm. long, 1–2 mm. wide; racemes 10–20 cm. long; flowers 10–12 mm. long, bracts deciduous, linear-filiform, conspicuously spreading-villous, pedicels 3–6 mm.; upper lip of calyx bifid, the lobes lanceolate, widely divergent, about 5 mm. long, 1 mm. wide, lower lip three-toothed, slender, about 6 x 1 mm.; petals bluish purple, banner reddish purple in center, broadly obovate to orbicular, about 11 x 11 mm., wings about 12 x 6 cm., keel slender, curved, 11–12 mm. long, ciliate on free edges below only; pods 20–30 mm. long, three- or four-seeded; seeds about 2 mm. long, tawny, marbled with dark brown, hilar area unmarked.

CALIFORNIA. Amador County: New York Falls, April, 1896, *G. Hansen 17* (US). Calaveras County: Murphey's to Sheep Ranch, May, 1895, *J. B. Davy 1561* (G, UC); Angels Camp, wooded hillsides, May, 1895, *J. B. Davy 1463* (G, UC). El Dorado County: Coloma, June, 1892, *E. Palmer 2391* (US); Pilot Hill, June, 1908, and April, 1915, *K. Brandegee* (UC); Placer-

ville, May, 1907, *K. Brandegee* (UC). Fresno County: Toll House, June, 1900, *Hall & Chandler 52* (UC). Kern County: Fort Tejon, 1857–8, *L. J. Xantus de Vesey 23* (G, US). Mariposa County: Mariposa Creek, April, 1903, *J. W. Congdon* (B); Pea Ridge road, June, 1883, April, 1901, and April, 1902, *J. W. Congdon* (US); same, April, 1903, *J. W. Congdon* (US 466505,

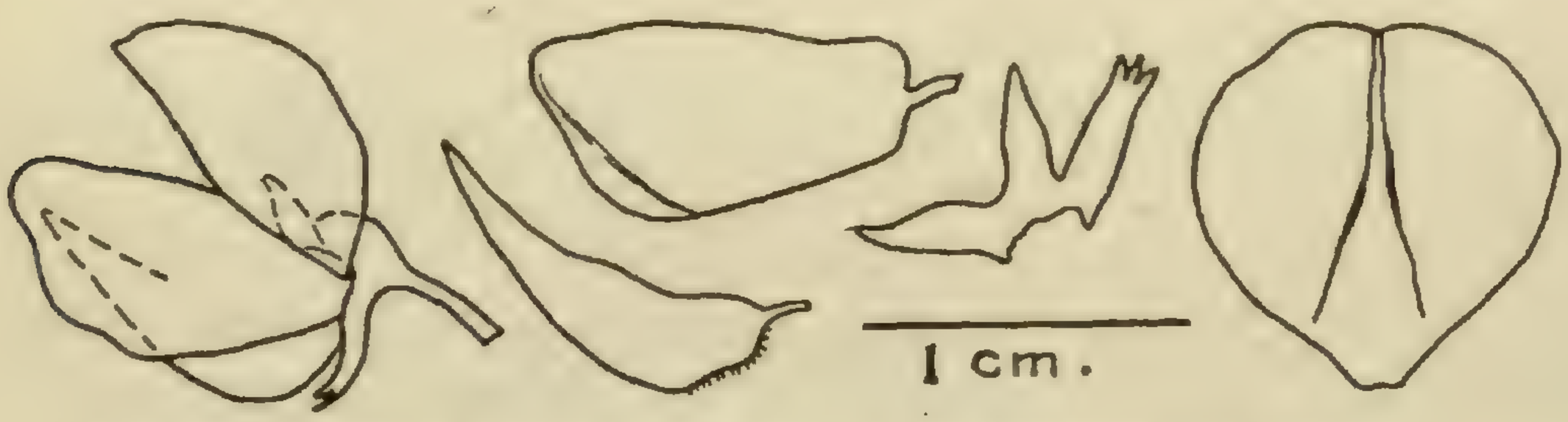

FIG. 63. LUPINUS BENTHAMI Heller. *J. W. Congdon* (US 466503).

left-hand specimen only). Monterey County: Stony Creek, Santa Lucia Mountains, May, 1897, *A. Eastwood* (G). Sacramento County: Folsom, April-June, 1883, *M. K. C.* (UC). Santa Barbara County: Alamo Creek, May, 1896, *A. Eastwood* (G). Tulare County: canyon above Grapevine Springs, April, 1898, *P. S. Woolsey* (G); Lemon Cove, May, *I. J. Condit* (UC); Three Rivers, May, 1894, *A. Eastwood* (G, UC). County not given: *J. M. Biglow* (G); *T. Bridges 58* (NY); 1891, *Mrs. E. P. Ames 31* (G).

This is a clean-cut species, easily distinguished from its nearest relatives. In more moist and richer soil it varies into a large robust form which seems to me to deserve recognition.

4*b*. **Lupinus Benthami opimus** var nov. [FIG. 64.]

A forma typica differt partibus omnibus grandioribus, pilis 2.5–3 mm. longis, caule paulo fistuloso, foliolis 2–3 mm. latis, longioribus, racemis 20–30 cm. longis, floribus 14–15 mm. longis, pedicellis 7–9 mm. longis, vexillo prope 14 mm. longo, 16 mm. lato, alis 14 x 10 mm., carina 14 mm. longa, curvatissima.

Differing from the typical form in all the parts being larger, excepting the calyx, hairs 2.5–3 mm. long, main stem more or less stout and fistulose; leaflets longer, 2–3 mm. wide; racemes 20–30 cm. long, flowers 14–15 mm. long, pedicels 7–9 mm. long; banner about 14 mm. long, 16 mm. wide, wings 14 x 10 mm., keel much curved, about 14 mm. long.

CALIFORNIA. Amador County: 1891, *G. Hansen* (UC). El Dorado County: Salmon Falls, May, 1909, *K. Brandegee* (UC). Kern County: Bakersfield, April-May, 1896, *J. B. Davy 1799* and *1926* (G, UC); Caliente, Walker's Basin grade, May, 1911, *K. Brandegee* (UC); Kern River bluffs, April, 1905, *A. A. Heller 7631* (B, NY, UC, US). Los Angeles County: Elizabeth Lake, Antelope Valley, May, 1896, *J. B. Davy 2654* (UC). Madera

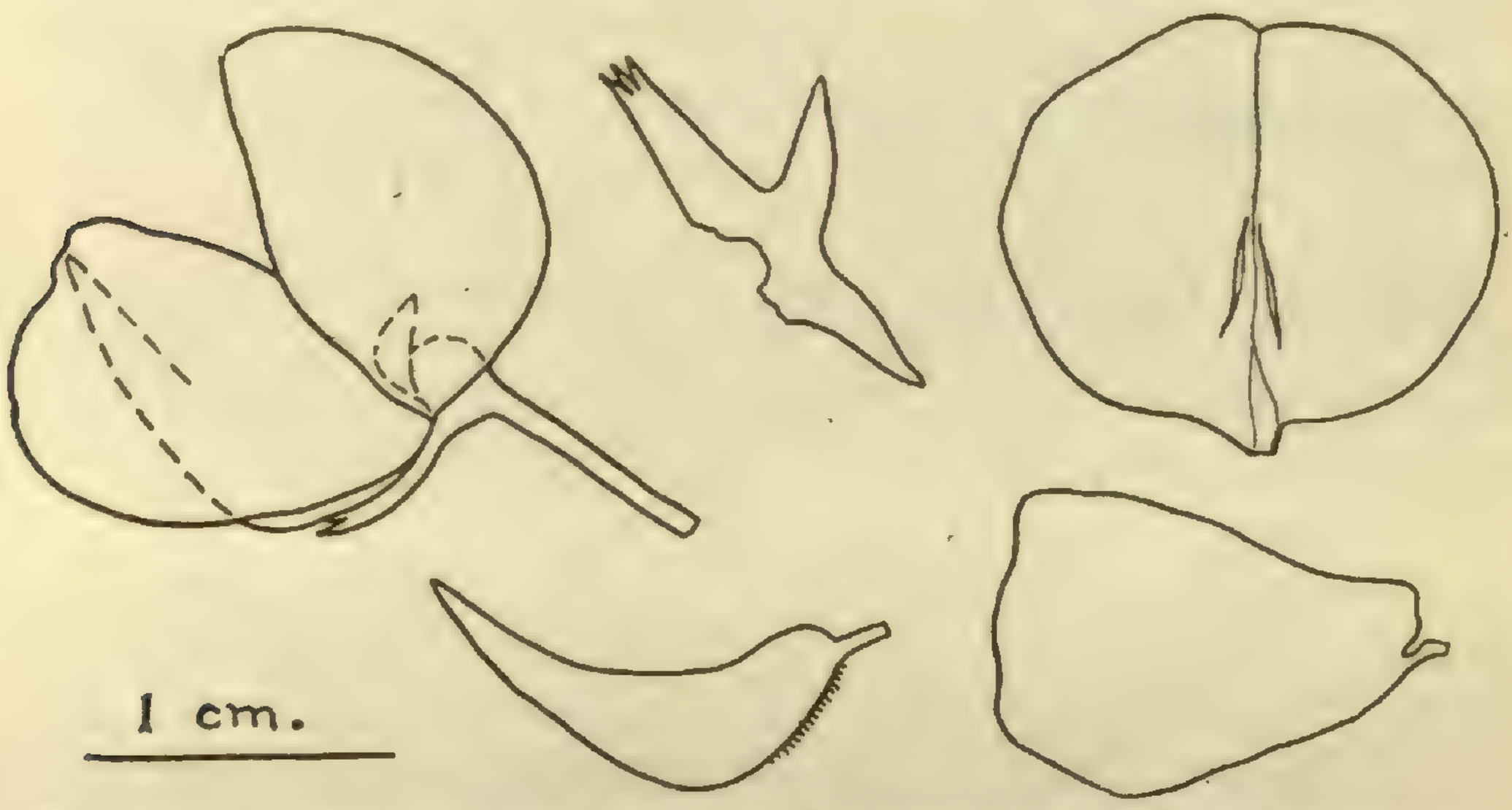

FIG. 64. LUPINUS BENTHAMI OPIMUS C. P. Smith. *A. A. Heller 8136* (US).

County: Pollasky, 11 April, 1906, *A. A. Heller 8136* (TYPE, B; type-duplicates, G, NY, US). Mariposa County: Pea Ridge road, April, 1903, *J. W. Congdon* (US 466505, right-hand specimen only). Placer County: Penryn, April, 1891, *C. F. Sonne* (UC). San Luis Obispo County: May, 1893, *Mrs. Blochman* (UC). Tulare County: Deer Creek, April, 1896, *C. A. Purpus 1703* (UC); Grapevine Springs, March, 1898, *P. S. Woolsey* (UC); Lindsay, March, 1897, *A. J. Hutchinson* (UC); hillsides, Middle Tule River, April-Sept., 1897, *C. A. Purpus 5671* (G, UC, US).

Opimus is Latin, here used in the sense of both "corpulent" and "splendid." Apparently this classification will care for a large majority of the specimens, very few real intermediates being evident.

5. LUPINUS CITRINUS Kellogg, Proc. Cal. Acad. Sci. 7: 93. 1877. [FIG. 65.]

Mostly 10–20 cm. tall, branched from the base, short-hairy; leaflets six to eight, oblanceolate, 15–20 mm. long, 2–4 mm. wide;

racemes 10–15 cm. long; flowers spreading in anthesis but soon deflexing, pedicels 3 mm. long, with spreading hairs; calyx with spreading hairs, upper lip bifid, its lobes about 3 mm. long and 2 mm. wide at base, lower lip minutely three-toothed, about 3–4 mm. long, 2 mm. wide; petals bright orange or golden, banner orbicular,

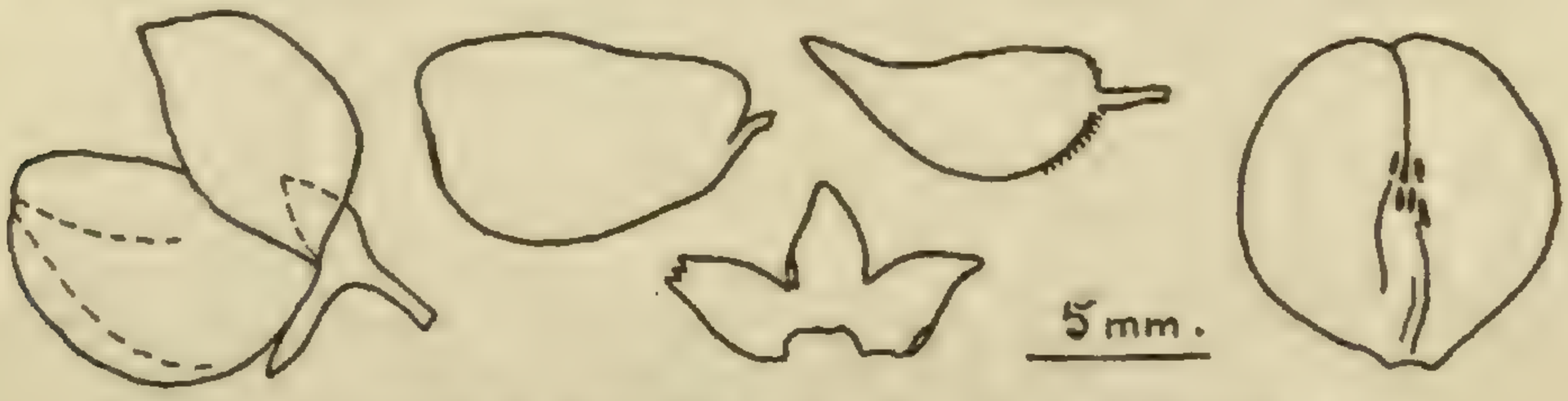

FIG. 65. LUPINUS CITRINUS Kellogg. *J. W. Congdon* (B).

emarginate, about 9 x 9 mm., wings 10 x 6 mm., keel nearly straight, ciliate on the lower free edges near claw; pods deflexed, practically glabrous, 12–15 mm. long, about 3 mm. wide, two- to four-seeded; seeds rhomboid, black-spotted on a pale ground, about 2 mm. long.

CALIFORNIA. Fresno County: Pine Ridge, June, 1900, *Hall & Chandler 119* (NY, UC); Toll House hill, May 1903, *J. W. Congdon* (B, UC).

Seemingly known only from Fresno County, where it was originally collected by E. Eisen. Kellogg refers to the keel as "naked," a character not supported by my findings in the case of the one dissection made by me; hence study of additional material is desirable.

6. LUPINUS DEFLEXUS Congdon, Muhlenbergia 1: 38. 1904. [FIG. 66.]

About 20–40 cm. tall, simple or branched from the base, pubescent, becoming glabrate; leaflets oblanceolate, about seven,

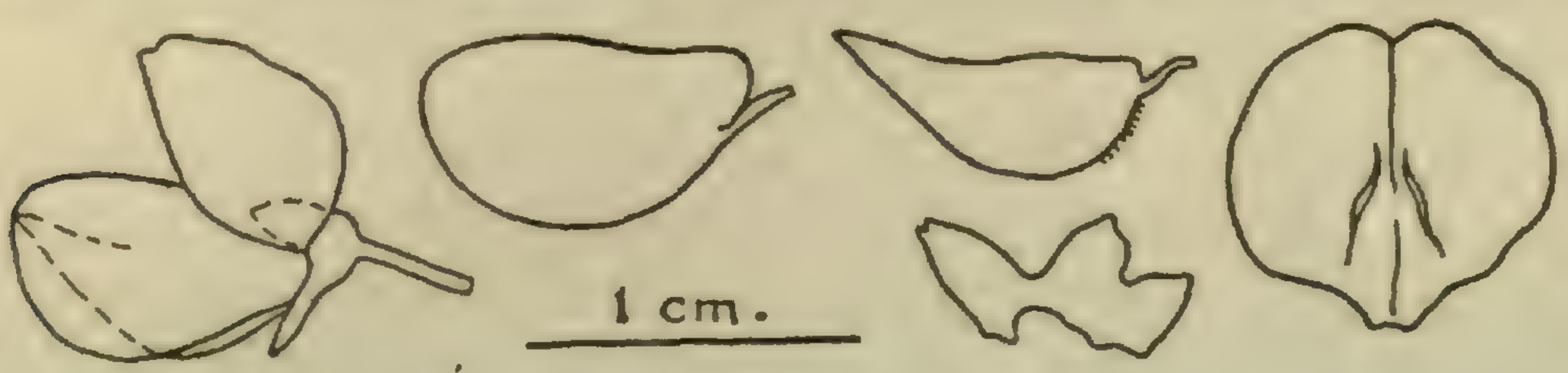

FIG. 66. LUPINUS DEFLEXUS Congdon. *J. W. Congdon* (US 466500).

15–25 mm. long, 3–5 mm. wide; racemes 6–20 cm. long; flowers spreading in anthesis, soon deflexing; pedicels 3–4 mm. long; calyx with spreading hairs, the upper lip two-lobed, the lobes

about 2 mm. broad, lower lip two- or three-toothed, 2 mm. wide, 4 mm. long; petals dull white or pinkish, banner suborbicular, emarginate at apex, about 10 x 10 mm., wings 10 x 6 mm., keel 9–10 mm. long, nearly straight, ciliate on the lower edges near the claw; pods about 20 mm. long, about 3 mm. wide, five- to eight-seeded, deflexed; seeds 2 mm. in diameter, smooth, unspotted, dull.

CALIFORNIA. Mariposa County: Mariposa Creek, near Mariposa, April, 1903, *J. W. Congdon* (B, G, UC); same, May, 1903, *J. W. Congdon* (B, G, UC, US).

Apparently confined to the type locality and collected by no one other than Mr. Congdon. Its nearest relative is *L. citrinus*.

In the citation of specimens the following abbreviations have been used in the present paper:

B, Brooklyn Botanic Garden;
CPS, private collection of the writer;
G, Gray Herbarium of Harvard University;
NY, New York Botanical Garden;
RM, Rocky Mountain Herbarium, University of Wyoming;
T, Torrey Herbarium (at New York Botanical Garden);
UC, University of California;
US, United States National Herbarium.

The vegetation of Connecticut.
VII. The associations of depositing areas along the seacoast *

GEORGE E. NICHOLS

(WITH TEN TEXT FIGURES)

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I. INTRODUCTION

In a previous paper of this series† the writer has discussed the plant associations of eroding areas along the Connecticut coast, and the present paper is practically a continuation of that one. As pointed out there, the lateral distribution of the various types of seaside plant association is determined mainly by differences in physiography, their vertical distribution mainly by differences in tide level. For purposes of treatment these associations are grouped primarily with reference to their physiographic relations, secondarily with reference to their relation to tide levels. A general discussion of the ecological relations of seaside plants and associations is included in the previous paper, which also contains a list of the literature cited in the present article.

The physical character of the shore and bottom in depositing

* Contribution from the Osborn Botanical Laboratory.

† NICHOLS, G. E. The vegetation of Connecticut. VI. The plant associations of eroding areas along the seacoast. Bull. Torrey Club 47: 89–117. *f.* 1–6. 1920.

areas varies with the degree of exposure and the nature of the tidal currents. In the more sheltered situations, as in embayments and behind barrier beaches, the deposit is mostly muddy; in less sheltered situations, as along parts of the shore which face on the open Sound, it is mostly sandy; in relatively exposed situations it may be stony. Broadly speaking, all portions of a depositing oceanic shore, which lie above low tide level and below the topographic form produced by agencies other than the sea, may be classed as beach.* Popularly, however, the term beach is generally applied only to sandy or stony shores, and in this sense it will be mainly used in the present paper, muddy shores (in so far as they are associated with the tidal marshes) not being classed as beach. As above defined, the beach includes only areas of water-deposited material; but the concept may conveniently be extended to embrace the contiguous areas of wind-blown sand which commonly overlie the higher portions of the beach proper. Beaches may take the form of spits and off-shore barriers, or they may fringe the mainland. In the latter case, the upper limit of the beach proper is usually marked by a line of bluffs or sand dunes.

II. THE VEGETATION OF DEPOSITING AREAS AND ITS ECOLOGICAL RELATIONS

A. STONY BOTTOMS AND BEACHES

1. Associations of the sublittoral region

There are occasional areas of stony bottom which seem to have originated through a process of aggradation rather than one of degradation, but it is well nigh impossible to draw sharp lines of demarcation between the two types. On the whole, stony bottoms are much more characteristically associated with eroding portions of the coast than with portions in which deposition predominates: in either case they are developed only in fairly exposed situations, and in both cases the character of the vegetation is essentially the same (see preceding paper of this series, p. 109).

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* In this connection, see especially discussion of Lake Michigan beaches by Cowles ('99, pp. 112 et seq.), of Long Island beaches by Transeau ('13), and of sand formations on marine coasts by Olsson-Seffer ('10a). Cowles, defining the beach in the sense given above, distinguishes between xerophytic and hydrophytic beaches. Transeau defines the beach as including "all of the areas occupied by the shore drift in transit."

2. Associations of the littoral and supralittoral regions

The associations of shingle beaches.—Along coasts which are open to the ocean, beaches of this description—built up very largely of water-rounded stones, ranging in size from pebbles up to cobbles six inches or more in diameter, that have been cast ashore by the heavy seas of winter storms—are the common type.* Even along the relatively sheltered Connecticut coast the beaches of comparatively exposed situations commonly are more or less gravelly or stony,† but typical shingle beaches are infrequent. The best example known to the writer is at Compo Beach, Westport—a rather surprising location, since it lies well toward the head of the Sound. Here there has been built up a stony spit, perhaps a hundred yards wide and rising five or six feet above ordinary high tide level, which extends out from the mainland about a quarter of a mile in a direction approximately at right angles to the southeasterly winds which here sweep unobstructed across the Sound. The windward slope of this spit is typical shingle, consisting, in the supralittoral, of pebbles and small cobbles.‡ Its vegetation is sparsely developed, comprising a small number of herbaceous xerophytes which grow scattered over the portion of the beach above high tide level. The following species are characteristic:

Chenopodium album
Atriplex patula hastata
Salsola Kali
Cakile edentula
Lathyrus maritimus
Solidago sempervirens
Ambrosia artemisiifolia
Xanthium canadense

On the lee slopes of the spit the substratum is a mixture of stones, gravel, and sand, and here the vegetation, while very open, is somewhat more luxuriant, including in particular a varied assort-

* Shingle beaches are well developed, for example, along the Cape Breton coast, where they have been described in some detail, with several figures, by the writer ('18, pp. 324–330).

† But the stony "beaches" which commonly are developed along the base of eroding bluffs of glacial drift are built up, not of materials washed ashore by the waves, but of boulders and stones, originally a part of the heterogeneous mass of rock waste which comprises the drift, that have been left behind when the finer materials were washed out and carried away by the waves. The gradual accumulation in this way of boulders along the base of an exposed bluff may come to form an effective protection against excessive wave action.

‡ It has not been possible to visit this beach at low tide, so that the littoral region has not been studied. Presumably its vegetation is similar to that of stony shores in the littoral as elsewhere described (Nichols, *l.c.*, p. 111).

ment of weeds. The following plants were noted as frequent or common, of the weeds only the more important being listed:

Juniperus virginiana
Poa compressa
Carex silicea
Polygonum aviculare
Polygonella articulata
Trifolium arvense
Lathyrus maritimus
Oenothera sp.
Trichostema dichotomum
Linaria vulgaris
Erigeron canadensis
Gnaphalium polycephalum
Ambrosia artemisiifolia
Achillea Millefolium
Artemisia caudata
Taraxacum officinale

Among other plants which ordinarily occur in similar situations elsewhere are the bayberry (*Myrica carolinensis*), the wild rose (*Rosa virginiana*), the cherry (*Prunus serotina*), various species of *Rhus*, and the mullein (*Verbascum Thapsus*).

B. SANDY BOTTOMS, BEACHES, AND DUNES

1. Associations of the sublittoral region

Sandy bottoms may be quite barren of vegetation, or they may support a usually scattered growth of eel grass (*Zostera marina*). This plant grows most luxuriantly on the muddy bottoms of sheltered waters, and its ecological relations will be discussed in connection with these; but it is apt to occur, locally at any rate, even in exposed situations, wherever there are deposits of sand or mud in which it can find foothold for its roots. Sand does not afford a favorable substratum for seaweeds; but as a rule these are represented by various of the species elsewhere noted as characteristic of eroding rocky or stony bottoms, here growing attached to shells or scattered stones, and also by forms which are epiphytic on the eel grass (see p. 523).

2. Associations of the littoral and supralittoral regions

Introductory.—Three subdivisions of the beach are commonly distinguished: the lower, the middle, and the upper beach. Along the seacoast, on sandy (or stony) depositing shores, the lower beach coincides approximately (but not exactly) with the littoral region, the middle beach with the lower supralittoral, the upper beach with the upper supralittoral.* These subdivisions are well brought out in FIG. 1.

* Olsson-Seffer ('10a) designates "that portion of the beach that lies below mean low tide, but which may be exposed by neap [*sic*] tides" as the "submerged beach," and terms the lower beach the "front beach."

Paucity of vegetation on the lower beach.—Edaphic conditions discourage the development of vegetation of any description on the lower beach along a sandy shore. Halophytic seed plants, such as characterize the littoral region along muddy shores, are unable to maintain a foothold in the shifting sand, constantly being worked over by the waves, and the algae likewise find conditions unfavorable. With local exceptions, the lower beach is virtually destitute of visible plant life.

FIG. 1. Sandy beach along relatively exposed seaward side of spit at Old Lyme; low tide. Upper limit of lower beach marked by line of tidal trash; middle beach here supporting very scanty plant population; dune beach (above) covered with *Ammophila*, etc.

Associations of the middle beach.—The lower beach is usually described as extending upward as far as the highest point reached by the waves of summer storms, and the middle beach as reaching from here to the upper limit of the winter storm waves. The actual position of these boundaries, of course, changes more or less from year to year. Because of the usual abundance of driftwood and other riff-raff, the middle beach is termed the "drift beach" by Jennings ('09). During summer this area

is undisturbed by wave action, but during winter it is frequently swept by the sea and sometimes becomes completely covered over with ice. Obviously conditions here are not suitable either for seaweeds or for perennial land plants. The characteristic inhabitants are xerophytic annual seed plants: species which in divers ways* are adapted to withstand the exposure to strong winds, intense illumination, and high temperatures to which plants growing on the open beach are constantly being subjected during the growing season.† The plant cover on the middle beach is

* Adaptation to a xerophytic environment on the part of beach and dune plants is seen particularly in their peculiarities of leaf structure. Thus, of the various species to be listed as characteristic of middle or upper beach, *Salsola*, *Cakile*, and *Arenaria* have leaves which are conspicuously succulent, *Atriplex* and *Lathyrus* have semi-succulent leaves, and *Xanthium* has hard, thick leaves; the leaf surface in *Chenopodium* and *Atriplex* is covered with a granular-waxy coating, and in *Euphorbia* and *Lathyrus* with a waxy "bloom;" the leaves of *Artemisia Stelleriana* are densely tomentose; while those of *Ammophila* are erect, stiff, and conspicuously involute. Moreover, in *Euphorbia* the entire aërial system of the plant exhibits a prostrate "radiant" habit—a habit also possessed, though to a less pronounced degree, by the shoot in several other beach plants. In addition to these peculiarities of the shoot system, which are associated either with the storage of water or its conservation (through reduction of transpiration), the root system in beach and dune plants is so developed as to make the most of the available water supply: a supply which, though scanty in the surface layers of sand, is usually quite abundant at depths of from six inches to a foot. The various annual species have a prominent tap-root, as have some of the perennials, and the usually abundant secondary roots radiate horizontally for considerable distances. Paucity of mineral and organic nutrients in the soil doubtless is a factor which markedly affects the character of beach and dune vegetation, and which may be largely responsible for the absence here of many plants that are found in dry soils elsewhere.

† For many years the plants of sea beaches, like those of salt marshes, were generally regarded as true halophytes. Kearney ('04), however, has shown that the amount of salt present in the sand of the middle and upper beaches at the height of the growing season is in reality very slight. At a station along the Massachusetts coast, in July, for example, the sand of the middle beach, near the lower limits of vegetation, was found to contain only 0.003 per cent, or less, of salt (as compared with 1.4–2.6 per cent in the soil of a nearby salt marsh). At certain seasons, of course, salt may be present in relatively large amount, but in regions of abundant precipitation it is rapidly leached out by percolating rain water. The plants of sea beaches, then, "are not generally halophytes, in the same sense that the plants of inland saline situations are, but are for the most part merely such plants of normally non-saline habitats as are able to withstand a high salt concentration without injury" (Bartlett, '09). Nevertheless, it is a fact, to quote further from Bartlett, "that a large proportion of the species of the beach and transition zone floras, although not necessarily always found within the limits of tide water, are, nevertheless, seldom found more than a few miles from the ocean." Bartlett suggests that it may be

best developed toward its upper margin, but even here, as a rule, the sand is only sparsely populated. Common species are the following:

Chenopodium album		*Salsola Kali*	*f*
" *leptophyllum f* *		*Cakile edentula*	*f*
Atriplex arenaria		*Euphorbia polygonifolia*	*f*
" *patula hastata*	*f*	*Xanthium canadense*	*f*
" " *littoralis*	*f*		

Associations of the upper beach.—The upper beach (FIGS. 1, 2) lies beyond reach of the waves at all seasons. Chronologically, it is the oldest part of the beach: it has been built up by wave-washed sands in former years, but is now protected by the middle and lower beaches.† As a habitat for plants the upper beach differs from the middle beach chiefly in its freedom from the mechanical effects of wave action, by reason of which it is possible for perennial species to exist here. The distinctive plants, frequently found also on the shoreward reaches of the middle beach, are four xerophytic perennial herbs: the sand reed or beach grass (*Ammophila arenaria*), the beach pea (*Lathyrus maritimus*), and, east of New Haven, the sandwort (*Arenaria peploides*) and the dusty miller (*Artemisia Stelleriana*). These, with various members of the middle beach flora, usually form a sparse, open covering over the sand.

Associations of the dune beach.—Along most sandy shores the upper beach, as a distinct topographic form, is practically absent,

necessary to alter somewhat our conception of what constitutes a halophyte, and that, while it may be impossible to correlate geographic ranges of beach plants with their adaptability to grow in highly saline situations, the possibility of some such correlation becomes greater if the ratio of saline constituents in the soil water, irrespective of their absolute concentration, be taken as a criterion, rather than absolute salinity. Thus a very slight admixture of sea water with an average soil water (in which the concentration of mineral salts is very slight) would be sufficient "to bring the ratio of elements into approximate agreement with sea water" (for further discussion, see Bartlett, *l. c.*, p. 223).

It is worthy of remark, in this connection, that a very considerable number of the plants which characterize the beaches and dunes along the New England coast are characteristic of similar situations along the Great Lakes, where soil salinity as an environmental factor is out of the question.

* Species marked "*f*" are characteristic of beaches along the Great Lakes.

† As with other portions of the beach, the lower boundary of the upper beach is subject to change, since in times of exceptionally severe storms the sea may sweep over areas which hitherto have been undisturbed by wave action for long periods.

since, almost invariably, all portions of the beach beyond reach of the waves quickly become covered over by aeolian deposits: by wind-blown sands which the on-shore gales catch up from the middle beach and sweep landward. In this way there originates what may appropriately be designated the *dune beach*: an area distinguished primarily by the presence of sand dunes.*

FIG. 2. Somewhat muddy beach along relatively sheltered landward side of spit shown in FIG. 1; tide not quite low. *Spartina glabra* forming an incipient marsh in midlittoral; *Ammophila* on dune beach above; intermediate beach nearly barren of vegetation.

Probably the finest dune beaches in the United States are those of the Lake Michigan region, the physiographic and ecological relations of which have been so admirably portrayed by Cowles ('99). There the dune areas constitute an important geographic feature, extending for long distances along the southern and eastern shores of the lake and in places reaching inland for more than a mile. These dunes frequently attain elevations of a hundred

* The term dune beach has been used by Ganong ('06) in a somewhat more restricted sense than that in which it is used by the writer.

and sometimes as much as three hundred feet. Similar dune complexes have been developed along various exposed shores on the Atlantic coast, as at Ipswich (see Townsend, '13) and Cape Henry (see Kearney, '01), but nothing comparable is to be met with along the relatively sheltered Connecticut coast. Here the dune beach ordinarily is little more than a broad, rounded, more or less continuous ridge of sand, from fifty to 250 feet wide, lying between the middle beach and the contiguous ordinary uplands, or, when developed on barrier beaches or spits (FIG. 2), separated from the mainland proper by lagoons or salt marshes. These low, ridge-like dunes seldom rise more than six feet above high tide level.* Their outer face usually is steep and irregular, due to the constant tendency which they exhibit to advance seaward, into the area occupied by the middle beach, where they become exposed, at periodically recurring intervals, to the battering of storm waves. The steep lee slopes characteristic of so many dunes are scarcely apparent in these low Connecticut dunes. Only occasionally is there developed more than a single dune, or line of dunes, and then the inner, shoreward dunes are scarcely worthy of the name.

But in spite of their geographic insignificance the dune beaches of the Connecticut coast are not without interest, and their vegetation has many points in common with that of more pretentious dune areas in other regions. As elsewhere along the northern Atlantic coast, the distinctive plant of the dune beach is the sand reed, which commonly predominates the landscape in all directions. But, although invariably foremost in abundance, and the species which primarily determines the aspect of the vegetation, this coarse grass never grows in sufficient density to crowd out other plants. Viewed at close range, its erect clumps of foliage are seen to be separated from one another by patches of bare sand, thus affording ample space for various other herbaceous species to develop, and these are present in locally varying abundance. Especially prominent in their effect on the general

* Larger and much more typical dunes are developed near Watch Hill, Rhode Island, but a few miles from the eastern boundary of Connecticut (see *f.* 1 in the preceding paper of this series). Some of these Rhode Island dunes are forty feet or more in height.

aspect of the vegetation are the beach pea, the evening primroses (*Oenothera muricata* and *O. Oakesiana*), the blazing star (*Liatris scariosa*), the seaside golden rod (*Solidago sempervirens*) and the wormwood (*Artemisia caudata*), to which may be added, among others, the following:*

Panicum amaroides
Triplasis purpurea
Eragrostis pectinacea
Cyperus filiculmis macilentus
" *Grayii*
Carex silicea
Polygonella articulata
Cakile edentula
Strophostyles helvola
Lechea maritima
Teucrium canadense littorale
Verbascum Thapsus
Erigeron canadensis
Gnaphalium polycephalum

As an environment for plants, the dune beach, during the growing season, is almost as unfavorable a habitat as the middle and upper beaches, and its vegetation is predominantly xerophytic. While the sand reed, with its herbaceous associates, usually predominates on the higher, more exposed sites, shrubs commonly occupy a prominent place in the more sheltered situations, as in the lee of the dune ridge, frequently forming dense thickets to the exclusion of much of the herbaceous vegetation. Particularly is this true of the beach plum (*Prunus maritima*), which usually is the most characteristic woody plant of the dune beach. The bayberry and the poison ivy (*Rhus Toxicodendron*) likewise grow in local profusion here, while the wild rose (*Rosa virginiana*) and sumacs (*Rhus* spp.) may be well represented. The false heather (*Hudsonia tomentosa*), a distinctive dwarf shrub of dune beaches in Rhode Island and elsewhere, is a comparative rarity along the Connecticut coast. Bryophytes and lichens are but sparingly represented by such species as *Ceratodon purpureus* and *Cladonia sylvatica*.

3. Successional relations along depositing sandy shores

The relatively rapid physiographic changes that ensue in the course of time along a depositing sandy shore, and the changes in the nature of the plant habitats which result, are accompanied by corresponding changes in the character of the vegetation, which

* From this list have been omitted various naturalized weeds which are characteristic of beaches, and also a number of comparatively rare native plants that belong here.

progressively increases in permanence and complexity. As the lower beach becomes built outward and upward, the gradually rising surface of sand becomes colonized first by the annual plants of the middle beach, which later are joined by the herbaceous perennials of the upper beach. With the development of the dune beach the plant population is still further augmented, and, under favorable conditions, shrubs may supplant herbs as the predominant growth forms. Only occasionally, in Connecticut, however, are trees met with on the dune beach, and forests never. In the development of the dune beach the vegetation itself plays an important rôle. The birth of a dune may be caused by the presence on the upper beach of any obstruction, such as a piece of driftwood, which interferes with the sand-laden winds sweeping landward, causing them to drop part of their burden. Thus, it commonly happens that the coarse, stiff, upright clumps of the sand reed, growing in local profusion on the upper beach and acting in the nature of a wind-break, bring about a local accumulation of sand and thereby inaugurate the development of a dune. But not only this. As the sandy surface is built upward, the grass, spreading by means of subterranean rhizomes, keeps pace with it, contributing further to the permanceny of the dune by the action of its copious slender roots, which bind the loose sand together, thereby fixing it in place.

C. MUDDY BOTTOMS AND SHORES, AND COASTAL SWAMPS

Introductory.—Among the outstanding physiographic features of the Connecticut coast is the extensive development of coastal swamps, typically represented by the salt marshes (FIGS. 4, 5, 6, 9). "Because of their lack of relief and uniformity of appearance", swamps of this description, in the words of C. A. Davis ('10), may appear "monotonous and uninteresting in the extreme"; yet it is only to the most superficial observer that they are entirely devoid of interest. Even as scenic features the monotony of the salt marshes is almost wholly one of topography, while from a scientific point of view these swamps, with their associated muddy flats and bottoms, present a diversity of fascinating problems, both biological and geological. According to figures given by Shaler ('85) there are fully 20,000 acres of coastal swamp in Connecticut.

In the account which follows, dealing primarily with the coastal swamps along the Connecticut shore, only those swamps are included whose vegetation is influenced, in some way or other, by the tides, or which are more or less intimately related to swamps of this type. As thus defined, coastal swamps along oceanic shores can be differentiated into three intergrading classes: *salt water swamps*, *brackish water swamps*, and *fresh water swamps*.* Salt water swamps are those whose surface is overflowed at more or less regular intervals (typically, twice each day) by practically undiluted sea water. Brackish water swamps are developed in situations where the inflowing tidal waters from the sea meet and intermingle with the outflowing fresh waters of inland streams or springs. Fresh water coastal swamps are developed either in situations where the ground is saturated with fresh water, derived from underground springs, and where the surface is overflowed so infrequently, or by saline water so dilute, that the freshness of the water in the soil is not affected; or else along the lower courses of rivers, in places where the influence of the tides in backing up the river water leads to the periodic inundation of the ground by fresh water.† The vegetation of salt and brackish water swamps in temperate regions is almost wholly herbaceous, consisting predominately of various grasses and grass-like plants. For this reason they are generally referred to as *marshes*. Popularly, both salt and brackish marshes are indiscriminately termed salt marshes. The vegetation of fresh water coastal swamps, in their most typical development, is likewise marshy, but some wooded swamps are also included in this group.

1. Associations of the salt marsh series

The muddy bottoms of the sublittoral.—The most distinctive plant of muddy bottoms along the seacoast is the eel grass (FIG. 3). As already noted, this also grows on sandy bottoms but it never attains there the luxuriance which it exhibits where growing on muddy bottoms. From mean low tide level, or slightly above,

* Shaler ('85, p. 361) distinguishes three classes of coastal swamps: salt water swamps, fresh water swamps, and estuarine swamps. From an ecological standpoint this grouping does not appear to the author as logical as the one here proposed.

† Swamps of the latter type are estuarine swamps, but so also may be the brackish swamps developed in similar situations further downstream.

the eel grass ranges downward to considerable depths, being recorded by B. M. Davis ('13) as growing in water as much as 75 feet deep in the Woods Hole region; but it is in the upper sublittoral that it flourishes best. So prolifically does it thrive in the shallow waters of protected harbors and coves that at low tide large areas of muddy bottom here will be almost completely hidden by its clusters of long, slender leaves. The eel grass is important on muddy bottoms, not merely because it is the dominant member

FIG. 3. *Zostera marina* on depositing bottom; leaves floating on surface at low tide. Orange.

of the flora, but also because it furnishes a substratum upon which many seaweeds, which otherwise would be absent, are able to grow. In the preceding paper of this series (*l.c.*, lists on pp. 102, 104), attention has been called to the fact that many of the algae of rocky bottoms grow also as epiphytes on the eel grass. These latter occur in association with the eel grass on muddy bottoms, some of them being more abundant here, at certain seasons, than on rocky bottoms. In addition to these, there are a number of the brown and red algae which grow exclusively as epiphytes on the eel grass, or more abundantly here than on any other type of substratum. Such are the following:

BROWN ALGAE (*Phaeophyceae*)

Punctaria latifolia

RED ALGAE (*Rhodophyceae*)

Chantransia virgatula
Callithamnion byssoideum
" *corymbosum*
Ceramium fastigiatum
Polysiphonia Harveyi
" *Olneyi*
Melobesia Lejolisii

But while algae may grow in great profusion on the leaves and stems of the eel grass, in the shallow waters of the upper sublittoral these attached forms may be overshadowed, both in mass effect and in ecological importance, by certain species which grow entirely unattached, notably by the enteromorphas and the sea lettuce (*Ulva Lactuca*). *Enteromorpha clathrata* in particular commonly grows as an epiphyte on *Zostera*, but these attached plants are usually small. Like *Ulva*, which germinates on rocks, piles and the like, just as soon as an attached enteromorpha plant reaches any size it is usually torn away from its support by currents or waves and thereafter is at their mercy. These free-floating plants commonly settle in large numbers in quiet shallow waters where they apparently find conditions exceedingly congenial to their further growth. The sea lettuce forms crumply sheets, commonly more than a foot and sometimes, according to Johnson and York ('15), as much as thirty feet in diameter. The enteromorpha similarly forms dense tangles which, with the sea lettuce, may cover large areas of bottom, sometimes to the exclusion of the eel grass. The ecological relations of the eel grass, sea lettuce and enteromorphas are discussed in detail by Johnson and York ('15, pp. 18 et seq.).

The tidal flats of the lower littoral.—In their treatment of the marine vegetation at Cold Spring Harbor, Johnson and York ('15) divide the littoral region into three sub-regions: the *lower littoral*, the *midlittoral* and the *upper littoral*. In the present account, thus far, little attempt has been made to differentiate between lower littoral and midlittoral, the former term having been used to cover both these divisions. But along muddy shores sharply defined differences in the character of the vegetation make such a distinction imperative. The lower littoral here may be defined as the region extending from approximately mean low tide mark upward nearly to half tide level: it embraces the stretch of "mud flats" which intervenes between the muddy bottoms

below, on which the aquatic eel grass is the character plant, and the salt marshes above, in which terrestrial grasses are the predominant forms. At ordinary low tides these tidal flats of the lower littoral present a surface of soft, blue-black, ill-smelling mud—an area in which, except for local colonies of eel grass or salt marsh grass (*Spartina glabra*), seed plants and attached algae are practically absent. At certain seasons these muddy flats may be destitute of visible vegetation of any description; but at others the bare mud at low tide is littered with loose sheets of *Ulva* and tangles of *Enteromorpha*, which may cover the ground so thickly that, when viewed from a distance, the surface appears verdant green. The failure of the eel grass to flourish on tidal flats is probably associated with its inability to withstand the desiccation and extreme temperatures to which plants growing here are frequently subjected at low tide. The influence of these factors must also react unfavorably on *Ulva* and *Enteromorpha*, but the loose carpet of vegetation which these form is constantly being renewed by fresh plants washed in by the tides and currents. The inability of the salt marsh grass, character plant of the next higher zone, to colonize the flats, is probably due to the inadequate aeration, particularly of its subterranean organs, at these lower levels (see detailed discussion in Johnson and York, '15).

The midlittoral marsh.—Salt marshes are typically developed on muddy bottoms, between approximately mean half and high tide levels, and their vegetation, taken in its entirety, is characterized by the predominance of perennial grasses or grass-like plants. The nature of the plant cover exhibits certain striking differences, however, primarily in relation to tide levels (FIG. 4). At the lower levels, in the region of greatest tidal play, the vegetation is made up largely of coarse, reedy grasses, between three and five feet tall; at the higher levels it consists mainly of finer, lower grasses and grass-like plants, mostly under a foot in height. The area occupied by the reedy grasses, extending from the lower limits of the marsh upward to within a few inches of the level reached by ordinary high tides (approximately to neap high tide level), may be designated the *midlittoral* or *reed marsh*; while the area occupied by the finer grasses, comprising the higher surface of the marsh, may be termed the *upper littoral marsh* or *meadow*.

In passing upward from tidal flats to midlittoral marsh there is a marked change, not only in the nature of the vegetation but in that of the substratum. The soft, structureless ooze of the lower levels gives way to a peaty or semi-peaty soil, muddy but relatively firm, composed partly of silt and partly of plant remains,

FIG. 4. Tidal creek, with border of *Spartina glabra*, and salt meadows. East Haven. View taken at low tide.

the whole being more or less compactly bound together by the thick underground stems of the reed-like grasses with their copious, long, slender roots. This transition ordinarily is quite abrupt. Commonly there is a low but distinct terrace-like effect where the midlittoral marsh impinges on the tidal flat, while along tidal creeks in particular the surface of the midlittoral marsh usually slopes sharply upward from the flats, forming steep banks frequently a couple of feet high. These steep banks are a direct result of the observed differences in substratum in relation to various agencies of erosion; for even along a shore where deposition predominates there is usually more or less local or periodic erosion associated with the shifting of tidal currents, the ebb and flow of

the water through tidal creeks, and the action of ice. The soft, unconsolidated mud of the flats offers little resistance to erosion, while the relatively firm, compacted soil of the midlittoral marsh withstands it to a considerable degree. It is only in situations where erosion phenomena are virtually negligible at all seasons that the transition between tidal flats and midlittoral marsh is gradual.

FIG. 5. *Spartina glabra* midlittoral marsh in New Haven harbor. View taken at high tide.

The character plant of the midlittoral marsh is the salt marsh grass (*Spartina glabra* vars. *pilosa* and *alterniflora*). This coarse grass everywhere forms a rank, fringing growth along the outer borders of the marsh and along the tidal creeks (FIG. 4). Ordinarily it occupies a narrow strip, a few yards wide at the most, but frequently, on gently sloping ground, it covers large areas (FIG. 5). Other seed plants are conspicuously absent from the midlittoral marsh, but the salt marsh grass seems peculiarly adapted to this habitat, where the ground is inundated, on an average, from five to sixteen hours daily and where, at the lower levels, the entire plant may become submerged at high tide. Toward the upper border of the midlittoral zone, however, the algae

may comprise an important element in the flora. *Vaucheria Thuretii* and *Rhizoclonium* spp. frequently form felt-like growths over the soft muddy substratum, or else, with other species, such as *Cladophora expansa* and *Enteromorpha clathrata*, build loose, tangled mats of vegetation. As at lower levels, loose plants of *Enteromorpha* and *Ulva*, drifting in with the currents and settling down amid the *Spartina* stalks, may maintain a more or less evanescent existence. The rockweeds (*Fucus* and *Ascophyllum*) may also be well represented in the upper reaches of the midlittoral marsh, either by loose specimens or by plants that have become partially buried in the mud and thereby fixed in place.*

The upper littoral marsh.—When viewed from a distance, the meadowy surface of the upper littoral marsh (FIGS. 4, 6, 9) appears to be flat, except where it is interrupted by the tidal creeks, which commonly meander through it, or by tidal pools and artificial drainage ditches. But the ground is not absolutely flat; invariably it is gently undulating. For the most part the differences in surface elevation are very slight (but an inch or a few inches at most), yet they are sufficient to have an important effect on the drainage and wetness of the marsh surface, on the aeration and salinity of the substratum, and thereby on the nature of the ground as an environment for plants.† The substratum here is firm and peaty, being made up largely of compactly interwoven rhizome and root remains.

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* The rockweed flora of salt marshes is of peculiar interest and has been the occasion of considerable study. Not only may these seaweeds, ordinarily associated with rock shores, form an essential part of the midlittoral salt marsh vegetation, but they develop here certain remarkable features which are not found elsewhere. In general these marsh-dwelling fucoids are characterized by their pronounced tendency to reproduce vegetatively, the absence of sexual reproduction, their dwarf habit, the lack of an attachment disc, and spirality or curling of the thallus. For detailed discussion and references to the literature, see Baker and Blandford ('16).

† The distribution of salt and brackish marsh plants is conditioned even more by the salinity of the soil water than by that of the water which floods the surface of the marsh. The salinity of the soil water is affected not only by the concentration of the water which overflows the surface of the marsh but by the length of time the surface is uncovered, the drainage relations, and by the presence or absence of subterranean supplies of fresh water. In a salt marsh at Cold Spring Harbor, Transeau ('13) found the salt content of the soil water in the *Spartina patens* association to be but 75 per cent as great as that of the harbor water, and in the *Juncus Gerardi* association but 57 per cent. See further observations by Bartlett ('09), Johnson and York ('15), Nichols ('18), and especially by Harshberger ('11).

Except locally, as along tidal creeks and ditches and in poorly drained depressions, the salt marsh grass is not present in salt meadows, where the ground ordinarily is flooded with saline water from but one to four hours daily, and then to a depth of only a few inches. Just what factors limit the upward distribution of this plant are uncertain. It may be the lessening salinity of the soil water (but, in this connection see remarks on p. 535); it may be the relative dryness of the soil at higher levels; it may

FIG. 6. Salt meadows, showing the billowy effect produced on the vegetation by winds and tidal currents. East Haven. *Juncus Gerardi* (right), *Spartina palens* (left).

be its inability to compete successfully with the salt meadow grasses; it may be a combination of factors (see Johnson and York, '15, pp. 48 et seq.) The predominant plants of the upper littoral marsh are three: the salt meadow grass (*Spartina patens juncea*), the alkali grass (*Distichlis spicata*), and the so-called black grass (*Juncus Gerardi*). These typically form a luxuriant meadow-like sward (FIG. 6). But while the three sometimes grow intermixed, they differ from one another in their ecological requirements

and, as a rule, one or another predominates locally. The salt meadow grass commonly comprises the bulk of the meadow vegetation, being especially characteristic of areas which are submerged several inches at ordinary high tides but where the water drains away rapidly between tides. The alkali grass is particularly characteristic of situations which likewise are submerged several inches at ordinary high tides, but where the water drains away more slowly than from the areas occupied by the salt meadow grass. The black grass thrives on the higher parts of the meadows, especially in areas which are barely reached by ordinary tides. It commonly forms a definite zone of vegetation along the landward borders of the meadow (see p. 533), though by no means restricted to this region.

Any one of the three species just mentioned may occupy considerable areas to the practical exclusion of everything else; but as a rule the grassy sward is dotted here and there with other seed plants which, if less abundant, are quite as distinctive. Particularly characteristic of salt meadows along the Connecticut coast are the following, any of which may grow in local profusion, especially in well-drained, relatively open situations where their grassy competitors are not too abundant:

Puccinellia fasciculata (Torr.) Bick.
Triglochin maritima
Atriplex patula hastata
Salicornia europaea
" *mucronata*
Suaeda maritima
Limonium carolinianum
Plantago decipiens
Solidago sempervirens
Aster subulatus
" *tenuifolius*

In addition to these, the salt meadow flora may include certain of the plants to be listed in connection with brackish meadows, these, however, being restricted in the main to the landward parts of the marsh. The character plants of salt meadows, like those of sea beaches, are distinctly xerophytic in their structure, and, except for the grass-like forms, all of them tend toward a succulent habit, the samphire (*Salicornia;* FIG. 8) being a leafless succulent of the most extreme type. Salt meadow plants apparently differ from beach plants,however, in being true halophytes: they are physiological rather than physical xerophytes.*

* Of special interest in the present connection is Kearney's paper ('18) on "Plant life on saline soils."

There is one peculiar feature of the upper littoral marsh which has already been suggested, and that is the occurrence, scattered here and there in greater or less abundance over the surface, of shallow depressions (FIGS. 7, 10), usually muddy or occupied by tidal pools at low tide, and strikingly different in the character of their vegetation from the adjoining higher and better drained parts of the meadow. These salt meadow pools and "rotten spots" (technically termed "pans"), the origin of which will be described

FIG. 7. Large pan in salt meadows becoming recolonized by local invasions of *Spartina glabra*. Westbrook.

later, may lack vegetation entirely, so far as the higher plants are concerned; and, while the alkali grass is frequently present, the salt meadow grass and the black grass are almost invariably absent. The character plants are usually two, namely the salt marsh grass and the samphire. Singly or in association, and not infrequently accompanied by the sea lavender (*Limonium*), these may predominate over considerable areas of undrained or poorly drained ground; but, even for them, the soil conditions are

not wholly favorable,* and very often they succumb to their manifestly unsuitable environment. The salt marsh grass, in such situations, commonly assumes a low, impoverished habit, often failing to flower, while the samphire and sea lavender grow much less vigorously than on better drained soils, frequently

FIG. 8. *Salicornia europaea* (right) and *Limonium carolinianum* (left). The smaller specimens of each grew in a poorly drained depression, the larger ones in a well-drained situation, in a salt meadow. New Haven.

exhibiting a very sickly appearance (FIG. 8). In the absence of seed plants, salt meadow pools may support a dense population of algae—*Cladophora expansa* and various species of *Enteromorpha*, together with numerous smaller and less conspicuous forms. The bottom in shallow pools commonly is overgrown by felt-like masses of blue green algae, comprising such forms as *Lyngbya*, *Oscillatoria*, *Microcoleus*, and *Chroöcoccus*, and in muddy depres-

* While there seems little question that the paucity of seed plants in salt marsh depressions is associated with poor drainage, it has not yet been established just what factors (aëration, salinity, etc.) are directly responsible for the failure of various halophytic species to grow here. See, in this connection, Yapp and Johns ('17, p. 97), Shreve, Chrysler, etc. ('10, p. 131).

sions the surface of the ground often is similarly covered by a thin, tough mat of intricately interwoven algae.* Various minute algae, or larger species that have been washed in, may be present elsewhere on the surface of the meadow, but they are of relatively subordinate importance in their effect on the general aspect of the vegetation.

The supralittoral region.—Locally, and particularly where it borders on the mainland, the surface of a salt marsh may rise above the level reached by mean high tides. Where not influenced by seeping subterranean fresh water, these higher, drier supralittoral portions of the salt marsh may maintain an almost pure growth of the black grass; or, particularly in the fresher situations, they may be populated by such species as the following:

Panicum virgatum
Hierochloë odorata
Spartina Michauxiana
Teucrium canadense littorale
Solidago sempervirens
Aster novi-belgii littoralis
Baccharis halimifolia
Iva oraria
Helianthus giganteus
Cirsium horridulum Michx.

The vegetation of the mainland, where it abuts on the marsh, may also be made up very largely of the species just listed, or the ordinary upland vegetation may fringe directly on the marsh. Even in the latter case, however, there are a number of species which are particularly characteristic of salt marsh borders. Among the trees the post oak (*Quercus stellata*) and the sour gum (*Nyssa sylvatica*) are deserving of special mention: the former reaches in southern New England its northern limit of range and, except locally, never extends inland; the latter, also near its northern limit here, is especially conspicuous along the edges of the salt marshes, where it stands out in early autumn by reason of the gorgeous red color of its foliage. Other woody plants which should be listed here are as follows:†

Juniperus virginiana
Smilax rotundifolia
Myrica carolinensis
Quercus bicolor
Celtis occidentalis
Sassafras variifolium

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*For further details regarding these algal felts and mats see B. M. Davis ('13), Johnson and York ('15), and Harshberger and Burns ('16).

† Favorable light relations probably are as important a factor as any in their influence on the character of the upland vegetation bordering salt marshes. Essentially all the species here listed are relatively intolerant of shade.

Pyrus melanocarpa
Amelanchier sp.
Rosa humilis
Rhus copallina
Rhus typhina
" *Toxicodendron*
Clethra alnifolia
Gaylussacia baccata

It very often happens that the ground along the edge of a salt marsh (supralittoral or upper littoral) is so saturated by underground fresh water that a swampy condition would prevail here, irrespective of the influence of tidal waters. In such cases the salt marsh proper is separated from the supralittoral fresh swamp by a region in which brackish marsh plants predominate. Many of these latter may extend well up into the supralittoral region, mingling here with the vegetation of the fresh water swamp (see later discussion of brackish swamps, etc.).

Muddy beaches.—Very often, in somewhat protected situations, the surface of an otherwise sandy or stony shore, in the littoral region, is somewhat muddy. Areas of this description (FIG. 2) can perhaps be regarded as incipient marshes, the actual development of typical marshland being prevented by currents or other local factors. The lower littoral along such a beach is frequently overgrown with salt marsh grass, although in other cases it is nearly barren, while the upper littoral usually supports various of the species characteristic of salt marshes, especially *Spartina patens*, *Salicornia europaea*, *Suaeda*, *Limonium*, and *Plantago*.

2. Associations of the brackish marsh series

The muddy bottoms and tidal flats of the sublittoral and lower littoral.—The eel grass commonly ranges well up into tidal creeks, but the characteristic plant of muddy bottoms in brackish waters is the ditch grass (*Ruppia maritima*), a form resembling the eel grass in general habit but much more delicate. This species also occurs here and there along the open Sound, in waters which are strongly saline (see Graves '08, pp. 122 et seq.), and, at the other extreme, it grows in waters that are only slightly saline. Even at its best, however, the *Ruppia* seldom approaches the more robust *Zostera* in mass effect. Another seed plant of shallow, brackish waters, sometimes growing in profusion and superseding *Ruppia* in the fresher waters, is the brackish water pondweed (*Potamogeton pectinatus*). In addition to these, *Vallisneria*

spiralis, *Zanichellia palustris*, *Potamogeton* spp., and various other aquatic seed plants of primarily fresh water habitats may extend seaward into waters that are perceptibly brackish. The algal flora of muddy bottoms and tidal flats in brackish waters lacks various of the species which elsewhere grow as epiphytes on *Zostera*, but the sea lettuce (*Ulva*) can grow in water which is quite fresh, and this plant, together with certain species of *Enteromorpha*, may make quite as prominent a display here as in the more saline situations.

The midlittoral marsh.—*Spartina glabra*, the character plant of the midlittoral region in salt marshes, exhibits a remarkably wide range of adaptability in relation to the salinity of the water which bathes its roots and shoots. Not only does it thrive in the most saline situations (generally speaking) but it is also capable of growing in habitats where the soil water is nearly fresh. Along the lower courses of fresh water streams it commonly reaches inland quite as far as the saline influence of the tidal waters, and in the majority of situations where the upper littoral region is occupied by brackish meadows the salt marsh grass maintains the commanding position in the midlittoral.* In waters which are but slightly saline the salt marsh grass comes into competition with such species as the bulrush (*Scirpus americanus*) and wild rice (*Zizania palustris*), but it is only where the brackish meadows and reed marshes of the upper littoral give way, upstream or inland, to fresh marshes that this grass becomes wholly replaced by other species. But one other plant need be mentioned here, viz., the water hemp (*Acnida cannabina*), a tall, stout, annual herb which is frequently associated with the *Spartina* in brackish waters, growing also at higher levels but principally along tidal streams.

Swamps of the upper littoral and the supralittoral regions.—The vegetation of the upper littoral region presents two fairly well defined aspects, namely, *meadow* and *reed marsh*. Brackish meadows are typically developed in the relatively more saline situations and differ little in general appearance from the true salt meadows of which they commonly are but continuations. Brackish reed marshes are best developed in the relatively fresher situations and

* It is a very common condition along tidal creeks, however, that the steep muddy banks of the midlittoral are practically destitute of seed plants.

are scarcely to be distinguished in general appearance from the fresh marshes into which they often merge. Between the brackish swamps of the upper littoral and those of the supralittoral it is impossible to draw any sharp line, and for this reason they have been grouped together. The supralittoral swamps (i.e., those beyond the reach of ordinary high tides) are distinguished chiefly by the greater abundance of plants which are associated primarily with fresh soil and by the practical absence of true salt marsh species. Most of the plants found here may be said to grow in fresh-to-brackish situations,† whereas most of the species of the upper littoral region may similarly be said to grow in salt-to-brackish situations (but some species of the upper littoral, such as *Solidago sempervirens*, are able to thrive in fresh as well as in saline soils). The appended remarks apply chiefly to the upper littoral.

Brackish meadows will be considered first. Locally and over considerable areas the salt meadow grass, alkali grass, and black grass, together with most of their associates in more saline situations, may be quite as prominent here as in salt meadows. Certain of the salt meadow species, particularly *Triglochin* and *Solidago*, are even commoner in brackish meadows, while but three of those listed on page 530, namely the two species of *Salicornia* and the *Limonium*, are perceptibly less frequent here. There is a marked tendency, however, for the salt meadow grasses to give way in brackish meadows to other grasses or grass-like forms, notably *Agrostis alba maritima*, *Eleocharis palustris*, and *E. rostellata*; and, especially in the fresher or higher parts of the meadows, these latter may predominate. Other seed plants which are more or less peculiar to brackish meadows, being found less frequently or not at all in typical salt meadows, are the following:

Cyperus Nuttallii
Scirpus nanus
Polygonum exsertum
" *aviculare littorale*
Spergularia marina
Potentilla pacifica Howell
Sabatia stellaris
Gerardia maritima
Pluchea camphorata
Iva oraria

Various of the bulrushes (*Scirpus americanus*, *S. Olneyi*, *S. campestris paludosus*, *S. robustus*) are locally abundant in brackish

† Plants which are capable of growing in either fresh or saline situations are designated "facultative halophytes" by Bartlett ('09).

meadows, growing in wet depressions and especially along the landward border of the meadow, in places where the ground is naturally very wet and swampy by reason of seeping underground water. In situations of the latter sort the vegetation bordering the meadow may be essentially that of brackish reed marsh (see below). Elsewhere, particularly where the substratum (upper littoral or supralittoral) is less wet and the ground water scarcely brackish much of the time, the meadow may be bordered by a fringe of predominantly lower vegetation, which includes, among others, various of the species listed below;* but there are all sorts of intergrading conditions:

Panicum virgatum
Hierochloë odorata
Cladium mariscoides
Carex hormathodes
Lilium superbum
Iris prismatica
Sanguisorba canadensis
Oenothera linearis
Cicuta maculata
Ptilimnium capillaceum
Samolus floribundus
Teucrium canadense littorale
Aster novi-belgii littoralis
Baccharis halimifolia
Iva oraria

Poorly drained depressions in brackish meadows may support a flora similar to those in salt meadows; or they may be occupied by *Triglochin*, *Plantago*, *Spergularia*, and various species of *Scirpus*. The physical nature of the substratum in brackish meadows, as a rule, is essentially like that of salt meadows—a compact peat rendered more or less gritty by inorganic sediment.

Brackish reed marshes frequently form fringing borders along the landward edges of brackish meadows, but they cover extensive areas only along the lower courses of large streams. In places of this description there commonly are broad tracts of land, away from the river, from which the water, by which the ground is overflowed at high tide, is prevented from draining away rapidly by a slightly higher ridge of ground (for convenience, here termed the *marginal embankment*) that borders the river itself on either side (see Nichols, '15, p. 171). These tracts are usually occupied by a dense growth of cat-tails (especially *Typha*

* It is of interest to note that while certain of the species here listed (e.g., *Iris prismatica*, *Baccharis halimifolia*, *Iva oraria*) are restricted to the vicinity of the seacoast, and while most of them are best developed here, the majority of them also are found in interior portions of this continent, particularly in the Mississippi basin and in the Great Lakes region.

angustifolia) or of the reed (*Phragmites communis*), together, particularly in the drier situations (as, for example, on marginal embankments) with the slough grass (*Spartina Michauxiana*). The rose mallow (*Hibiscus Moscheutos*) often occupies a prominent position here, as also along the landward edges of brackish meadows, and the wild rice may predominate in the fresher situations.

The swamps of the *supralittoral region* may be essentially similar in their vegetation to the brackish meadows and marshes which have just been described; but swampy situations in the supralittoral, even where exposed to periodic inundation by somewhat brackish water, are often wooded. As already suggested, the explanation of this fact, as well as of the occurrence, on drier but occasionally overflowed uplands adjoining both salt and brackish meadows, of various trees, shrubs, and herbaceous plants which are distinctly non-halophytic, seems to be this: that "while the surface marsh soil may be strongly saline, the subsoil is controlled by fresh water which flows outward from the higher ground under the salt marsh sod" (Harshberger, '11, p. 487). In the case of many plants which thus appear to be flourishing in an essentially halophytic environment, it may therefore be only the shoots—organs which are incapable of absorption and hence but little affected—that are actually exposed to the unfavorable influence of the saline water.

Muddy tidal shores.—In addition to the plants described in preceding paragraphs, there are a number of forms which are generally described as growing along muddy tidal shores rather than in the marshes. These plants are especially characteristic of brackish tidal shores along rivers, and for the most part are rather local in their occurrence. The following are representative:

Lopholocarpus spongiosus
Heteranthera dubia
Ranunculus Cymbalaria
Tillaea aquatica
Lilaeopsis lineata
Limosella aquatica

3. Associations of the fresh marsh series

Introductory.—Fresh water coastal swamps may be either marshy or wooded. Wooded coastal swamps scarcely differ from wooded swamps inland and merit no special comment here, but the fresh water marshes of the coast present certain distinctive

features. Particularly is this true of marshes which are of estuarine origin, and these will be taken as representative of the fresh water series. *Fresh water estuarine marshes* occur along parts of fresh water streams which are subject to tidal fluctuations but are beyond the influence of saline waters. They may occupy low grounds of any description, but are most typically developed in situations which are topographically similar to those elsewhere occupied by brackish reed marshes. Along the Connecticut and Quinnipiac rivers they make their appearance a few miles above the river's mouth, further upstream passing into flood plain swamps.*

The sublittoral region.—The vegetation of the river bottom below low tide level comprises various aquatic seed plants, especially the wild celery (*Vallisneria spiralis*) and divers pondweeds (*Potamogeton* spp.). Locally, in quiet waters, the water lilies (*Nymphaea advena* and *Castalia odorata*) may be abundant. Other common aquatics, such as the water weed (*Elodea* sp.) and *Najas flexilis*, are variously represented. The bottom vegetation is well developed only in shallow, slow-flowing waters.

The lower littoral and midlittoral marsh.—The character plant here is the wild rice (FIG. 9). Along muddy stream borders and in sloughs, in water ranging from a few inches to more than two feet deep at high tide, this magnificent grass, sometimes nearly ten feet high, commonly forms a luxuriant growth. With it, especially in the shallower water, may grow various of the species listed below:

Sparganium spp.
Sagittaria latifolia
" *graminea*
Echinochloa Walteri
Leersia oryzoides
Scirpus americanus
Peltandra virginica
Orontium aquaticum
Pontederia cordata
Polygonum acre
Sium cicutaefolium
Bidens laevis

* Here, as elsewhere, the transition from one type of swamp to another is gradual, and there are all intermediate degrees between the typical salt marshes which prevail near the mouth of the river and the typical flood plain swamps which characterize portions of the river above tide water. As in the salt marshes, the substratum in an estuarine marsh, whether brackish or fresh, usually is more or less peaty, but any attempted line of demarcation between fresh estuarine swamps and flood plain swamps, where the substratum is practically pure alluvium, must be quite arbitrary.

On the whole these latter plants are of relatively subordinate ecological importance, but certain of them, e.g., *Orontium*, frequently predominate locally.

FIG. 9. *Zizania palustris* fringing an estuarine marsh along the Quinnipiac River. North Haven.

The upper littoral marshes and meadows.—In typical cases the vegetation of the upper littoral region, which includes the greater part of the swamp surface, is predominately reed-like in the vicinity of the river and in the lower situations, tending to assume a meadow-like aspect away from the river and in the higher situations. Of the reed-like forms, the cat-tails (*Typha latifolia* and *T. angustifolia*) are the commonest representatives, and the cat-tail associations, together with the wild rice associations of the wetter situations, comprise the most distinctive association-types of *estuarine fresh marshes*.* The following plants, among others, are commonly associated with the cat-tails in fresh coastal marshes, either as scattered individuals or as local dominants:

* Harshberger ('19) likens marshes such as these to the British "fens," and proposes that they be so designated.

Aspidium Thelypteris
Phragmites communis
Scirpus validus
" *cyperinus*
Iris versicolor
Juncus brevicaudatus
Rumex Brittanica
Impatiens biflora
Hibiscus Moscheutos
Cicuta maculata
Lysimachia terrestris
Lycopus spp.

The vascular plants in the subjoined list may be taken as representative of the flora of *estuarine fresh meadows*, as well as of coastal fresh meadows elsewhere. The list is far from complete.

Onoclea sensibilis
Osmunda cinnamomea
Calamagrostis candensis
Carex stricta
Juncus effusus
Lilium superbum
Polygonum arifolium
Polygonum sagittatum
Verbena hastata
Galium Claytoni
Eupatorium purpureum
" *perfoliatum*
Aster novi-belgii
" *puniceus*

Any of these meadow species may also grow in association with the cat-tails, as may certain of the forms listed for the midlittoral region. Fresh water cat-tail marshes, like the meadows, are by no means restricted to estuarine situations, but are variously distributed along the coast.

The supralittoral region.—There is only one portion of the supralittoral that merits special comment, and this is the marginal embankment. Although the height of the surface here is but slightly greater, as a rule, than that of the upper littoral marsh, which it tends to cut off from the midlittoral marsh along the river, the difference in elevation and drainage may be quite sufficient to have a marked effect on the vegetation. Not only are sundry herbaceous plants found more frequently here than elsewhere, but the marginal embankment often stands out conspicuously by reason of its woody vegetation. Shrubs and trees may occur scattered locally through parts of the marsh away from the river, but along the channel they commonly form a prominent fringe of vegetation. The trees here include the willows (*Salix nigra*, *S. alba vitellina*), the elm (*Ulmus americana*), and various other species elsewhere characteristic of flood plains or river swamps. A list of representative herbaceous and shrubby species is given below.

HERBACEOUS SPECIES

Phalaris arundinacea	*Vernonia noveboracensis*
Spartina Michauxiana	*Mikania scandens*
Elymus spp.	*Aster paniculatus*
Lobelia cardinalis	*Ambrosia trifida*

SHRUBS

Salix lucida	*Cornus Amomum*
" *longifolia*	*Clethra alnifolia*
Alnus rugosa	*Cephalanthus occidentalis*
Rosa carolina	*Sambucus canadensis*
Ilex verticillata	*Viburnum dentatum*

4. Successional relations along depositing muddy shores

Introductory.—In discussing this phase of the subject attention may be confined to the salt marshes, brackish and fresh marshes being neglected. Generally speaking, a salt marsh seems to originate through the accumulation of silt and organic debris at lower levels and the consequent elevation of the substratum to a height at which the salt marsh grass is able to establish itself. Except for the prominent part played here by the accumulation of silt, the manner in which muddy bottoms along the seacoast become built up is essentially similar to that in which many lakes become filled in during their conversion into swamps (see Nichols, '15). There is a close analogy to the early stages in the development of a flood plain (see Nichols, '16), except that, in the present case, vegetation plays a more active part and the inorganic debris is much finer. Plants assist in the building-up process in two ways: first, through their mechanical interference with tidal currents, retarding these and causing them to deposit their load of silt; second, through the accumulation of their own dead remains.

The apparent succession of plant associations.—Assuming our salt marshes to have originated in the manner just suggested, it would very naturally be inferred that as the substratum has been gradually built up to successively higher elevations and as the environmental conditions of the habitat have thereby undergone progressive alteration, the rising ground has been successively occupied, in order, by the associations (or groups of associations) elsewhere described as characteristic of the sublittoral, the lower littoral, the midlittoral, and the upper littoral regions. In other words, it would seem that the historic succession of plant associa-

tions during the development of the marsh must have followed the same order as the zoned series of associations which is to be encountered along the outer edge of most marshes, in proceeding from the muddy bottoms of the sublittoral upward to the grassy meadows of the upper littoral. As will be brought out presently, however, this hypothetical correspondence, though formerly accepted as a fact (see Shaler, '85, etc.), would seem to be merely apparent.

The actual succession of plant associations and its probable explanation.—In attempting to work out the successional relations of any given series of plant associations there are various methods of procedure, but all of those customarily employed necessarily are based on the study of the existent vegetation. In the large majority of cases, therefore, conclusions regarding the nature of any given successional series, where this extends over a period of time beyond that during which the area in question is actually under observation, must be founded wholly on circumstantial evidence. It is of course inevitable that any deductions regarding the future course of succession should be largely hypothetical, and, except in the comparatively few instances where historic records are available or where a fossil record has been left by successive generations of preëxistent plants, any reconstruction of the course of events in the past must likewise be largely assumed from theoretical deductions. Salt marshes, however, resemble peat bogs in that conditions have favored the preservation of a fossil record, since they are usually underlain by peat deposits which may extend to a depth of many feet, and the study of these salt marsh peat deposits has yielded some very significant facts.

Assuming the vertical or historic order of succession during the development of the marsh to have been coördinate with the present day lateral sequence of zones, as set forth in the second paragraph above, the peaty and mucky deposits underlying a salt marsh should show approximately the following sequence of layers, from below upward: (1) a layer of silt, with remains of eel grass, extending from a variable depth to low tide level; (2) a layer of silt, with but few vegetable remains, extending from low tide level up to the level at which the salt marsh grass becomes established; (3) a layer of muddy peat with more or less abundant

remains of salt marsh grass, extending upward nearly to mean high tide level; (4) a layer of peat made up largely of the remains of the salt meadow grasses. But the actual examination of sections of salt marsh peat along the New England coast has revealed a very different state of affairs. Bartlett ('09), for example, describes a salt marsh near Woods Hole in which the salt marsh peat near the surface is underlain by the remains of a former *Chamaecyparis* bog, the stumps of large numbers of trees being preserved *in situ*. C. A. Davis ('10) reports that in the vicinity of Boston the peat deposits underlying the salt marshes likewise consist, in many cases, of the remains of fresh water vegetation; in other cases peat deposits composed largely of the remains of salt meadow grasses extend from the surface downward to a depth below that of mean low tide level—in other words, to a depth many feet lower than that at which the plants which formed the peat could possibly have grown. In no case, Davis emphatically states, does the peat show the hypothetical arrangement of layers specified above. The peat underlying a brackish meadow near New Haven, and sectioned during operations for brick clay, shows similar conditions: just beneath the surface (1) a thick layer of *Spartina patens-Juncus Gerardi* peat, followed in order below by (2) a layer of *Distichlis* peat and (3) a layer made up largely of cat-tai and fern remains, with (4) numerous scattered stumps resting in place on the underlying gravelly substratum, about five feet below the present mean high tide level.

From the foregoing observations it is clear that any assumed agreement between the present-day zonation of salt marsh associations in relation to tide levels and the succession of plant associations which has ensued during the development of the marshes, along the New England coast, is not in harmony with the facts as recorded by the underlying peat deposits, in so far as these records have been made available. By most authors, including Ganong ('03), Penhallow ('07), Bartlett ('09, '11), C. A. Davis ('10), Townsend ('13), and Johnson and York ('15), this discrepancy is explained as being due to coastal subsidence, abundant evidence (botanical and otherwise) tending to indicate that the land along the Atlantic coast has been gradually sinking at the rate of a foot or more per century. It is quite obvious that subsidence at a

rate more rapid than that at which the marsh surface is being built up would lead to an order of succession more or less completely the reverse of the apparent order earlier outlined, i.e., the succession of plant associations would be retrogressive; and, further, that a rate of subsidence exactly counter-balancing that at which the marsh surface is being built up would favor a complete absence of change in the character of the surface vegetation, i.e., there would tend to be no succession whatever. Only where the rate of upbuilding exceeds that of submergence could the actual succession of plant associations be expected to coincide with the apparent succession, i.e., only under these conditions could a progressive succession take place; and whether any such correlation ever actually exists remains to be demonstrated. The coastal subsidence explanation for the invasion of fresh swamps by salt water, and similar phenomena, is scouted by D. W. Johnson ('13), who would account for the observed facts in other ways; but Johnson's arguments are not wholly convincing.

Origin of salt marsh depressions, or "pans."—Mention has been made in an earlier paragraph (p. 531) of the occurrence, particularly in the meadows of the upper littoral, of poorly drained depressions, which differ greatly in the character of their vegetation from adjoining portions of the marsh (FIGS. 7, 10). The origin of these depressions, which range in depth from a fraction of an inch to well over a foot, has been variously accounted for. Harshberger ('16) attributes them to masses of tidal trash (consisting commonly of dead stems and leaves of eel grass and salt marsh grass, but in many cases—see Johnson and York, '15—made up largely of loose-floating *Ulva* and *Enteromorpha*) which in times of exceptionally high water are swept in over the surface of the meadow by tidal currents and, settling down there (particularly in places where the vegetation already has become matted and twisted by winds and waves, as shown in FIG. 6), smother out the existing plant cover. Subsequently, he maintains, rapid decay sets in, affecting not only the aerial plant organs but the underground parts as well, and eventually a depression of some depth may thus arise. This explanation, which is also suggested by Johnson and York ('15, pp. 21, 22, 47, etc.), accounts in a wholly satisfactory manner for the origin of the essentially flat barren spots, which are of frequent

occurrence in salt meadows, and a similar explanation accounts, in large measure, for the presence in the midlittoral marsh, in areas otherwise densely populated by salt marsh grass, of open patches (see FIG. 5), bare and muddy at low tide and frequently of considerable dimensions. It may perhaps account also for the origin of some of the shallower depressions in the meadows of the upper littoral; but many, if not most, of these latter, and the majority, if not all, of the deeper depressions, have arisen in a very

FIG. 10. Development of pans through local invasion of tidal creeks and ditches by *Spartina glabra*. Westbrook. In view to right a former meandering creek has become quite obliterated. Ditch in center has become completely obstructed; the one to left is still open.

different manner. Recent detailed studies by Yapp and Johns ('17) on the origin of these "pans" (as the depressions are termed by them and by other European ecologists) in the salt marshes of the Dovey Estuary, in Wales, have fully confirmed conclusions which the writer had already reached regarding their origin in the salt marshes along the Connecticut coast.

Avoiding detail, as far as possible, the pans of the upper littoral meadows may be divided into two groups, with reference to their mode of origin: primary pans, which are formed during the development of the marsh; and secondary pans, which arise subsequently. *Primary pans* are formed in somewhat the following manner. During the early development of the marsh, the

salt marsh grass, instead of forming a zone of vegetation directly continuous with that at higher levels along the shore, frequently grows in a more or less continuous belt at some little distance offshore, being separated from the higher portions of the shore by an area, of variable width but sometimes as much as a dozen yards across, or even more, in which the ground is practically destitute of seed plants (this condition is suggested in FIG. 2).* As the portion of the shore occupied by the grass becomes built upward, this plantless portion lags behind, eventually giving rise to a water-filled depression in the mature marsh. In one of the Cape Breton salt marshes studied by the writer (see Nichols, '17, FIG. 45; also Harvey, '19, FIG. 3) these depressions have persisted in the mature marsh as elongated lagoons of open water. But more commonly they become broken up and in part obliterated, during the growth of the marsh, through local invasions of the salt reed grass: indeed, small areas commonly become hemmed in by the salt reed grass at a very early stage in the development of the pan. *Secondary pans* may arise in several ways, one of which has already been described. In many cases (FIG. 7) their formation results from the relatively rapid building up of the ground along the margins of tidal streams, with the consequent ponding back of the water, between tides, in the lower parts of the meadow, away from the stream (see, in this connection, Nichols, '15, pp. 171, 172; also p. 537 of the present paper). Very commonly, also, they arise through the local invasion and obstruction of shallow tidal creeks by the salt marsh grass, a method of development graphically brought out by FIG. 10. Occasionally they seem to originate as ox-bows, in the usual manner, from meandering tidal creeks.

The fate of these pans need not be traced in detail. Unchanging though it may appear, the surface of a salt marsh, from year to year, is in a constant state of alteration. Erosion here and deposition or peat accumulation there tend to bring about changes in drainage and elevation which in turn react on the vegetation. In the shifting course of events the pans of today are destined, sooner or later, to vanish, while other areas, now occupied

* The absence of plants here is commonly due to the periodic accumulation along the shore of wave-washed drift, after the manner already described (pp. 545, 546).

by typical salt meadow vegetation, may become transformed into pans. And, in conclusion, it is needless to more than remark that, as a result of artificial ditching operations, which have become more and more prevalent in recent years, the pans, a natural breeding place for mosquitoes, are destined to undergo even more rapid changes than those above suggested.

Acknowledgments.—The manuscript, both of the present and of the preceding paper of this series, has been read by Dr. E. H. Eames, Dr. A. W. Evans, Dr. C. B. Graves, Mr. C. A. Weatherby, and the late Dr. F. S. Collins, to all of whom the writer is indebted for criticism and suggestions.

SHEFFIELD SCIENTIFIC SCHOOL,
YALE UNIVERSITY

INDEX TO AMERICAN BOTANICAL LITERATURE

1916–1920

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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Stapf, O. *Ribes niveum*. Bot. Mag. *pl.* 8849. 1920.

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BULLETIN

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TORREY BOTANICAL CLUB

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Rocky Mountain botany and the Long Expedition of 1820

GEO. E. OSTERHOUT

With July, 1920, a hundred years had passed since Major Long made his notable expedition to the Rocky Mountains. In the spring of 1819, on May 6th, the expedition left Pittsburgh in a specially constructed steamboat named Western Engineer, and during the summer made its way down the Ohio River, up the Mississippi, and up the Missouri to the mouth of the Platte at Council Bluffs. Here the company wintered and remained till June, 1820, when Major Long arrived, and on the 6th of June the party began its journey up the Platte. Dr. William Baldwin started with the expedition as botanist, but he was seriously ill and died at Franklin on the Missouri, August 21, 1819. With Major Long came Dr. Edwin P. James, who became botanist of the Expedition, and geologist and surgeon, and also its historian. Traveling as rapidly as possible, collecting was a difficult matter, and yet Dr. James was able to make a notable collection of botanical specimens. Not only were the specimens many in number, but there were many of unusual interest because they were new species. Pursh and Nuttall had already discovered and published many of the peculiar plants of the Rocky Mountain region, but Dr. James was first to ascend above timberline and collect among the alpine flora.

On June 22d the Expedition arrived at the junction of the North with the South Platte. The barren and sterile character of the country is often noted, and on the 29th, when in

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the vicinity of where Fort Morgan now is, Dr. James observed: "The cactus ferox reigns sole monarch, and sole possessor, of thousands of acres of this dreary plain. It forms patches which neither a horse nor any other animal will attempt to pass over." On the next day the first glimpse of the Rocky Mountains was noted. Almost the whole of July was passed in the mountains or in their vicinity. The company hoped to reach the mountains for the 4th of July, but the day found them journeying along the South Platte in the vicinity of the mouth of the St. Vrain Creek. "Several valuable plants," Dr. James observes, "were here collected and, among others, a large suffruticose species of lupine." The only species of *Lupinus* which Dr. Torrey described from the collection was *L. decumbens*, and its habitat was said to be, "on the southern branches of the Arkansas." It may have been collected again, but since what I suppose is *L. decumbens* Torr. is quite common in this section, this is probably the species mentioned. July 5th the Expedition camped opposite the mouth of "Cannon-ball Creek," now Boulder Creek, and on July 6th, at noon, camped where the Platte emerges from the mountains, and remained there till the morning of the 9th. Among the many plants collected in this vicinity were *Geranium caespitosum* James, and *Acer glabrum* Torr. On July 11th, as the company halted for the dinner time, our beautiful blue columbine, *Aquilegia coerulea* James, was collected. This was just after crossing the divide toward where Colorado Springs is, and on the afternoon of the same day *Stanleya integrifolia* James was found. On the 12th the company camped on "Boiling-spring Creek," now Fountain Creek, not far from the site of Colorado Springs. "Near this encampment," in the words of Dr. James, "we first observed the great shrubby cactus, which forms so conspicuous a feature in the vegetable physiography of the plains of the Arkansa." Here also he mentions "a cucurbitaceous vine, resembling some of our common squashes, bearing a small pepo, which is round and smooth, and as large as an orange."

On the morning of the 13th Dr. James with two companions left camp to make the "ascent to the summit of the peak," Pikes Peak. They ate dinner at the "boiling spring," Manitou, and "halted at sunset in a small cluster of fir trees," near a brook.

The account continues: "On the morning of the 14th, as soon as daylight appeared, having suspended in a tree our blankets, all our provisions, except about three pounds of bison's flesh, and whatever articles of clothing could be dispensed with, we continued the ascent, hoping to be able to reach the summit of the peak, and return to the same camp in the evening. . . . The day was bright, and the air nearly calm." At about twelve o'clock they arrived at timberline. "A little above the point where the timber disappears entirely, commences a region of astonishing beauty, and of great interest on account of its productions. The intervals of soil are sometimes extensive and covered with a carpet of low but brilliantly-flowering alpine plants." Here was a most interesting moment; new and undiscovered plants—things of the greatest interest to the botanist—were about them, but time and daylight failed. "We met as we proceeded, such numbers of unknown and interesting plants, as to occasion much delay in collecting; and were under the mortifying necessity of passing by numbers we saw in situations difficult of access. . . . It was about 4 o'clock P.M. when the party arrived on the summit. At about five in the afternoon the party began to descend, and a little before sunset arrived at the commencement of the timber." Shortly after they were obliged to stop for the night without reaching the camping place of the preceding evening. On the next morning, Dr. James continues, "we had traveled about three hours when we discovered a dense column of smoke rising from a deep ravine on the left hand." The camp-fire had not been extinguished, and it started a fire which destroyed nearly all the provisions and the bedding and clothing, which had been left at the camp. They arrived a little after noon at the "boiling spring."

This was undoubtedly the most notable day of the Expedition for botanical collecting, both from the standpoint of the number of new species discovered, and from the fact that it was an introduction to the rich and beautiful alpine flora of the central Rocky Mountains. The new plants—nearly all alpine—were: *Apinus flexilis*, *Alsinopsis obtusiloba*, *Heuchera bracteata*, *Telesonix Jamesii*, *Trifolium nanum*, *T. dasyphyllum*, *Oreoxis humilis*, *Primula angustifolia*, *Drosace carinata*, *Mertensia alpina*, *Penstemon alpinus*,

Chionophila Jamesii, *Castilleja occidentalis*, and *Tetraneuris brevifolia*. *Mertensia ciliata* and *Besseya plantaginea* must have been collected near this date and may have been found about Pikes Peak. The last is Bentham's *Synthyris plantaginea*, but I suppose it was first described by Dr. James in the "Catalogue of Plants" which he contributed to the American Philosophical Society, as *Veronica plantaginea*, though he observed that it was "unlike in habit and appearance to the American Species of *Veronica*." Near this date, too, he must have collected the *Pentstemon* which he lists in the "Catalogue of Plants" as "*P. coccineum* N. S.?", though he offers no descriptlon of it. Evidently it was a bright red *Pentstemon*, and I suppose it was the only one which Bentham later described as *P. Torreyi*.

On July 16th the Expedition moved from the vicinity of Colorado Springs to the bank of the Arkansas river where Pueblo now is. On the 17th Captain Bell with Dr. James and two other men ascended the Arkansas to the present site of Canyon City. Little of interest is noted in botanical collecting for the trip. On the morning of July 19th "we turned our backs upon the mountains, and began to move down the Arkansa." When about a hundred miles down the river the party divided. Captain Bell with the greater part of the Expedition continued down the Arkansas, while Major Long, accompanied by Dr. James and eight other men, turned southward toward the Canadian River. During the journey of the first day, July 24th, at the noon encampment were collected *Rudbeckia* (now *Ratibida*) *Tagetes* James and *Sida* (now *Sphaeralcea*) *stellata* Torr. The next day they came to the Purgatory River, up which they traveled, and camped on its bank or that of a tributary for the night. Dr. James writes: "A beautiful dalea, two or three euphorbias, with several species of eriogonum, were among the plants collected about this encampment. Notwithstanding the barrenness of the soil and the aspect of desolation which so widely prevails, we are often surprised by the occurrence of splendid and interesting productions springing up under our feet, in situations that seemed to promise nothing but the most cheerless and unvaried sterility."

On the 27th they extricated themselves from the rocky canyons of the Purgatory River, where traveling had been exceedingly

difficult, and took "without the least regret our final leave of the 'valley of souls in purgatory.'" They came out onto a high table-land, and the next day came to a stream which they came to consider as a tributary of the Canadian River. Under date of July 30th Dr. James wrote: "The country between the sources of the Purgatory creek and the stream on which we are now encamped is a wide and elevated formation of trap rocks, resting on horizontal sandstone. In traversing it we had collected many new and interesting plants. Among these were a large decumbent mentzelia, an unarmed rubus, with species of astragalus, penstemon, myosotis,* helianthus, etc." It would seem quite probable that *Penstemon Jamesii* Benth. was among the pentstemons collected at this time. From Dr. James's descriptions it seems evident that the country traversed during the last few days of July was the southeast part of Las Animas County, Colorado, and adjacent New Mexico; and the first streams encountered were tributary to the Cimmaron River and not to the Canadian. Through this piece of country there is an extensive area of extrusive igneous rock, which is often mentioned in Dr. James's descriptions as trap rock. The plants collected would be indigenous on both sides of the boundary line between Colorado and New Mexico. The reference to "Sources of the Canadian" may apply equally to tributaries of the Cimmaron. After this date many other plants were collected, but the expedition passed eastward, out of the Rocky Mountain region and the plants are more of southern and eastern affinities.

The new species were described by a number of botanists; some by Dr. James, most of them by Dr. Torrey, a few by Torrey and Gray, and a few by the English botanist Bentham. Dr. James furnished a Catalogue of Plants, except the critical species, to the American Philosophical Society, which was "read" August 17, 1821, and published in 1825. Dr. Torrey published most of his new species in the Annals of the New York Lyceum of Natural History, from 1824 to 1826; some of the proceedings seemingly were not published till 1828. Dr. James made his classification according to the Linnaean system, but Dr. Torrey published his "Account" according to the natural system, the first publication so made in the United States.

* The species of "myosotis" may have been of *Lappula* or *Oreocarpa*.

To know the locations where Dr. James collected many of his specimens is not an easy matter. His "Account" of the expedition is a narrative of its daily progress, and when plants are mentioned in the narrative it is an easy matter to determine the location; but only a few of them are so mentioned. In the published lists no dates are given, and the localities of the new species are often indefinite. While the following list is probably quite incomplete, it is a remarkable list of new species, all or nearly all of them collected as the Expedition crossed the territory now comprised in the state of Colorado; and seemingly the first botanical collection which was made in this territory. The species are arranged according to the sequence in Rydberg's "Flora of the Rocky Mountains and adjacent plains," published in New York, 1917, the names follow this work throughout with the original synonyms cited where necessary.

Andropogon Torreyanus Steud. (*Andropogon glaucus* Torr. not Muhl.)
Pleuraphis Jamesii Torr.
Aristida fasciculata Torr.
Sporobolus airoides Torr. (*Agrostis airoides* Torr.)
S. cryptandrus (Torr.) A. Gray (*Agrostis cryptandra* Torr.)
Apinus flexilis (James) Rydberg (*Pinus flexilis* James)
Populus angustifolia James
Celtis reticulata Torr.
Eriogonum umbellatum Torr.
E. Jamesii Benth.
E. tenellum Torr.
Quamoclidion multiflorum Torr. (*Oxybaphus multiflorus* Torr.)
Paronychia Jamesii T. & G.
Alsine Jamesiana (Torr.) Heller (*Stellaria Jamesiana* Torr.)
Alsinopsis obtusiloba Rydb. (*Arenaria obtusa* Torr. not All).
Aquilegia coerulea James
Stanleya integrifolia James
Cristatella Jamesii T. & G.
Heuchera bracteata (Torr.) Seringe (*Tierella bracteata* Torr.)
Telesonix Jamesii (Torr.) Raf. (*Saxifraga Jamesii* Torr.)
Edwinia americana (T. & G.) Heller (*Jamesia americana* T. & G.)
Opulaster monogyna (Torr.) Kuntze (*Spiraea monogyna* Torr.)
Oreobatus deliciosus (Torr.) Rydb. (*Rubus deliciosus* Torr.)
Hoffmannseggia Jamesii T. & G.
Lupinus argentea Pursh (*L. decumbens* Torr.)

Trifolium nanum Torr.
T. dasyphyllum Torr.
Parosela formosa (Torr.) Vail (*Dalea formosa* Torr.)
P. Jamesii (Torr.) Vail (*D. Jamesii* Torr.)
Astragalus mollissimus Torr.
Geranium caespitosum James
Tragia ramosa Torr.
Acer glabrum Torr.
Sphaeralcea cuspidata Torr. (*Sida cuspidata* Torr.)
Frankenia Jamesii Torr.
Oenothera Jamesii T. & G.
Anogra coronopifolia (T. & G.) Britton (*Oenothera coronopifolia* T. & G.)
Galpinsia lavendulaefolia (T. & G.) Small (*Oenothera lavendulaefolia* T. & G.)
Gaura parvifolia Torr.
Primula angustifolia Torr.
Drosace carinata (Torr.) A. Nels. (*Androsace carinata* Torr.)
Asclepias speciosa Torr.
A. latifolia (Torr.) Raf. (*A. obtusifolia* var. *latifolia* Torr., *A. Jamesii* Torr.)
Gilia longiflora (Torr.) G. Don (*Cantua longiflora* Torr.)
Phacelia integrifolia Torr.
Oreocarya suffruticosa (Torr.) Greene (*Myosotis suffruticosa* Torr.)
Mertensia ciliata (Torr.) Don (*Pulmonaria ciliata* Torr.)
M. alpina (Torr.) Don (*P. alpina* Torr.)
Phyla cuneifolia (Torr.) Greene (*Zapania cuneifolia* Torr.)
Melosmon laciniatum (Torr.) Small (*Teucrium laciniatum* Torr.)
Scutellaria resinosa Torr.
Quincula lobata (Torr.) Raf. (*Physalis lobata* Torr.)
Solanum Jamesii Torr.
Penstemon alpinus Torr.
P. Jamesii Benth.
P. ambiguus Torr.
P. Torreyi Benth.
Chionophila Jamesii Benth.
Besseya plantaginea (Benth.) Rydb. (*Synthyris plantaginea* Benth.)
Castilleja occidentalis Torr.
Plantago eriopoda Torr.
Vernonia marginata (Torr.) Raf. (*V. altissima* var. *marginata* Torr., *V. Jamesii* T. & G.)
Isocoma pluriflora (T. & G.) Greene (*Linosyris pluriflora* T. & G.)

Tonestus pygmaeus (T. & G.) A. Nels. (*Stenotus pygmaeus* T. & G.)
Leucelene ericoides (Torr.) Greene (*Inula ericoides* Torr.)
Ratibida Tagetes (James) Barnh. (*Rudbeckia Tagetes* James)
Thelosperma gracile (Torr.) A. Gray (*Bidens gracilis* Torr.)
Tetraneuris brevifolia Greene (*Actinea integrifolia* Torr. not Kunth)
Gaillardia pinnatifida Torr.
Pectis angustifolia Torr.
Artemisia filifolia Torr.
Ptiloria tenuifolia (Torr.) Raf. (*Prenanthes tenuifolia* Torr.)
P. pauciflora (Torr.) Raf. (*Prenanthes pauciflora* Torr.)

In general the native plants still grow and blossom as they did when Dr. James saw them in 1820; but a great change has been wrought in the country. Fruitful farms have replaced much of what seemed to be sterile soil, and towns and cities and a busy industry have come to their silent and uninhabited plains and hills.

WINDSOR, COLORADO

Geographical distribution of the marine spermatophytes

WILLIAM ALBERT SETCHELL

The marine spermatophytes belong to two nearly related families, the Hydrocharitaceae and the Potamogetonaceae. The members of both families are aquatic, either inhabiting the fresh waters or those which are brackish or marine. Of the first family, the Hydrocharitaceae, there are three genera, *Halophila*, *Enalus* and *Thalassia* which are marine, while of the second family, the Potamogetonaceae, there are five marine genera, viz., *Zostera*, *Phyllospadix*, *Cymodocea*, *Diplanthera* (or *Halodule*) and *Posidonia*. Of these eight genera, I find thirty-four or thirty-five species at present enumerated. Undoubtedly much is yet to be learned concerning the marine spermatophytes since they have not been so generally collected and studied as other spermatophytes because of their habitat. The greater number of the species, in fact all except the three species of *Phyllospadix*, so far as I am aware, live in shallow water (down to not over 10 fathoms usually) and are seldom if ever uncovered by ordinary low tides. Such localities are seldom visited or collected over by botanists other than phycologists and the latter are usually in search of "other game." There are only two botanists who have given special attention to the marine spermatophytes, viz., P. Ascherson and C. H. Ostenfeld. The former interested all explorers, travellers and navigators possible in these plants and obtained much that was valuable as a result of his and their efforts. As early as 1867, Ascherson published a preliminary account of the marine spermatophytes as then known. He published supplementary accounts in 1870, 1871 and 1875. Finally he contributed the account of the marine genera to Engler and Prantl's "Pflanzenfamilien" (1889) and of the marine species of the Potamogetonaceae to Engler's "Pflanzenreich" (1907). In 1871, Ascherson also discussed the geographical distribution of the "sea-grasses," as he designated the marine spermatophytes and later (1906) issued a revision of this article bringing the information and dis-

cussion up to date. The greatest credit is due to Ascherson for following up the subject for so many years and with such vigor as well as for the very satisfactory way in which he has treated these little-known plants. Within comparatively recent years Balfour (1878) has written concerning the morphology of *Halophila* and Rydberg (1909), concerning the morphology of *Thalassia testudinum* Solander, while Ostenfeld (1905, 1908, 1909 and 1916) has contributed several papers dealing with the morphology, taxonomy and ecology of members of both families of marine spermatophytes.

The ecology, or topographical distribution, of the marine spermatophytes is fairly simple and more or less uniform in the principal details. They all grow in shallow water, that is from about high-water mark down to ten fathoms and possibly in exceptional cases even somewhat deeper. The species of *Phyllospadix* are usually inhabitants of the lower and even middle littoral belts, but they differ in other details of their ecology from the rest of the marine spermatophytes (cf. Dudley, 1893, p. 415). The species other than those of *Phyllospadix*, are inhabitants of the upper sublittoral belt and are seldom completely uncovered unless it is at the time of extreme low-water. The species, also with the exception of those of *Phyllospadix*, at least so far as known to me, prefer comparatively quiet water and are most often found in sheltered places although some, at least, are found in runways where there may be at times fairly swift and strong currents. The species of *Phyllospadix*, on the other hand, prefer localities within the littoral belt where they are exposed to strong wave action and foaming surge (cf. Dudley, 1893, p. 415) and may be classed as typical "surge-plants" or "cumaphytes." As to substratum, the great majority of the species grow with their long and prostrate rhizomes buried more or less deeply in the sand or mud, but *Posidonia oceanica* and the species of *Phyllospadix* inhabit rocky, or stony, ground and have comparatively short and more or less erect and condensed rhizomes. The method of dissemination of *Phyllospadix* is one of the very few of those of the marine spermatophytes known. This was worked out in the botanical laboratory of the University of California a number of years ago by Ralph E. Gibbs (1902). He was the first to describe

the ripened and detached fruits. After the pulpy exocarp is worn away from the ripe drupe-like fruit, there remains the black horn-like mesocarp exposed to view. The fruit, in this condition, looks like the head of some large beetle with two projecting and inwardly curved but unjointed antennae, or possibly mandibular structures. The inner edges of these arms, which come off at an acute angle from the sides of the flattened turbinate main body of the fruit, have inwardly and upwardly pointing stout fringing bristles. By means of these arms and their bristly armature, the fruit, floating in the waves may grasp a jointed coralline on the otherwise bare and smooth rock and tightly cling to it. It may also germinate in position on the coralline and, as the rhizome develops, it sends out a quantity of stout roots from each segment. The roothairs, which are produced in abundance, attach themselves to the rocks and also catch and hold floating sand, and this process continues as the rootstock goes on developing until a small patch of sand is formed about the developing plant. A small beach may thus be formed among the rocks. This behavior makes it evident by what method the *Phyllospadix* obtains its foothold and maintains it on the exposed rocky shores where it, alone of all the marine spermatophytes, can make its home. The mud- and sand-inhabiting species are distributed over wide areas by the plants and portions of plants, especially those having portions of the rhizomes or ripened or ripening fruits, which are torn away, or dislodged in some fashion, and float long distances, as happens so constantly and on such a large scale in the case of *Zostera marina* (cf. Ostenfeld, 1908, p. 6, 15) and in very special form in *Cymodocea antarctica* (cf. Tepper, 1881). As to the salinity and specific gravity of the water in which the marine spermatophytes grow, it is probably enough to state that the designation "marine" is intended to convey that the plants included are inhabitants of salt as distinguished from brackish water and that the variation in salt content is comparatively slight (cf. Ostenfeld, 1908, p. 17, and Osterhout, 1917).

The topographical conditions and considerations just enumerated have to do with the various marine spermatophyte or "*macrenhalid*" formations and associations found in various zones, regions, provinces and districts of the marine flora, but it is the

intention of this paper to inquire rather into the climatic distribution of the marine spermatophytes and to compare it with the distribution of the marine algae: In attempting to do this, I shall try to arrange the different species in the climatic zones already outlined by me in previous papers (1915, 1917). These climatic zones are as follows:—Upper Boreal and Upper Austral of mean maximum temperatures from 0°–10° C., Lower Boreal and Lower Austral 10°–15° C., North Temperate and South Temperate 15°–20° C., North Subtropical and South Subtropical 20°–25° C., and Tropical from 25° C. mean maximum up to the limit of 29° or 30° C. It seems that the marine spermatophytes ought to follow the same temperature laws as the marine thallophytes and be found in similar zones and just as closely restricted in their distribution. The algae, so far as I am able to determine at present, are either restricted to a single zone or, if they extend from one zone into others, invade the additional zones because, for some reason or other, they find in the invaded zone, or zones, the temperatures characteristic of the zone to which they are normal. The reasons for suspecting invasion, even when the data are not completely at hand for proof is the existence of warm areas, spots and particularly of seasonal minima in warmer zones each with its peculiar flora. Since the marine spermatophytes inhabit the shallow waters, the criteria of their distribution may be considered to be the mean maxima and minima of the surface waters 5° C. apart, as it is in the case of the great majority of the marine algae.

The climatic distribution of the marine spermatophytes has been treated of by Ascherson as I have already mentioned. In 1871, he published his paper on this subject and discussed and represented on maps the distribution of the twenty-two species then known to him. In distribution by oceans, Ascherson credits one species to the Arctic Ocean, seven to the Atlantic, fourteen to the Indian Ocean and thirteen to the Pacific Ocean. The Antarctic Ocean has no species credited to it. Ascherson discusses the relation of the different species to the climatic zones as laid off with reference to the Arctic Circle and the Tropics of Cancer and Capricorn. Such a discussion of climatic distribution does not lead very far even in connection with land plants, since

the relation either to isotherms or to the total amount of heat obtained is not shown with any exactness. Ascherson, also, in charting the distribution, simply draws a continuous line between the extreme records and makes an enclosed area as if of continuous occurrence and of possibly uniform frequency. The results are, consequently, confusing and misleading. It is, nevertheless, a simple matter in the case of the strictly tropical species. They are in the great majority among the marine spermatophytes and are clearly shown as inhabitants of the warmer, or even of the warmest waters of the oceans. The distribution in cases of the smaller number of inhabitants of the temperate zones, as these are understood and marked off on the ordinary maps seems also plain, although here it is difficult to understand in the case of certain of these species why they do not fill out their "zones" more completely. One species, however, shows such an extensive distribution as to cause special remark on the part of Ascherson. This is the common "eel-grass" of our Atlantic coast, *Zostera marina*. As plotted by Ascherson, this species extends from the Kara Sea (to the northwest of Asia) down to Cadiz in Spain, from Iceland to Newfoundland (avoiding Greenland) and thence down the eastern coast of the United States to western Florida, from Bering Strait to and including Yakutat Bay, Alaska, and from the same strait down along the east coast of Asia through the Loo Choo Islands nearly, but not quite, to Formosa. Such an extensive distribution might well disturb any ideas of limits of distribution at all narrow.

In the revised reprint of his paper, issued in 1906, Ascherson lists thirty-two species of marine spermatophytes, an increase of ten over the earlier issue, some of which had resulted from segregation from species listed before, and also expresses doubt as to the extreme limits of the distribution of *Zostera marina*. He still lays stress, however, on the circles and the tropics in their relation to the distribution of the individual species.

In 1907 Ascherson contributed the accounts of the marine spermatophytes, so far as published, to the "Pflanzenreich" of Engler, and Ostenfeld, in 1902, published a preliminary revision of *Halophila*. From these, as well as from other sources, it seems that some thirty-four or thirty-five species are now to be recog-

nized. Of these eighteen are confined to the tropical zone of marine waters as I have attempted to limit it by including only those waters of a mean maximum temperature of 25° C. or above, four to subtropical zones in that they inhabit marine waters of a mean maximum of 20° to 25° C., while four are inhabitants of strictly temperate zones, whose mean maxima range from 15° to 20° C. These twenty-six species certainly seem typically stenothermal, being limited to zones of amplitudes of 5° C., for the hottest month of the year, as to their persistence. The remaining eight species are reported as extending over two or more zones (of 5° C. mean maxima each) and consequently, therefore, more or less eurythermal. Of these one species is credited with occupying both tropical and subtropical zones, five species with occupying both subtropical and temperate zones, one species as occupying tropical, subtropical and temperate zones, while one species is credited with occupying both boreal zones as well as temperate, subtropical and tropical zones or five zones in all. The last species is, if properly referred to all the zones it is said to inhabit, a most typically eurythermal species. It seems best, however, to inquire into the particulars of the distribution of these seemingly eurythermal species and to attempt to determine so far as possible the exact conditions underlying the attributing to them of such extensive ranges.

The cases of species credited with inhabiting two zones do not seem very difficult of explanation on a strictly stenothermal basis. In other words, such species may be found to belong strictly to one or other of the zones they inhabit and invade the second zone only because they find at certain places, or at certain seasons, the same heat conditions that they need and find in the normal zone. To examine into difficult cases, we may select *Zostera capricorni* Ascherson, which is said to extend from Cape York in tropical eastern Australia to Port Jackson in subtropical eastern Australia. It will needs be uncertain until this species is better known, as to just which zone is to be considered normal for this species, but the distribution indicates that the South Subtropical Zone is the normal zone since *Z. capricorni* extends only partially into the Tropical Zone. The invasion of the Tropical Zone, in this case, may be seasonal and this supposition is strengthened by observing

that the isocryme, or line of mean minimum temperature for 25° C., touches the coast of eastern Australia in the vicinity of Cape York. In the cases of the five species which are credited to both a subtropical and an adjacent temperate zone, two of these species, viz., those belonging to the genus *Phyllospadix*, are not certainly members of the flora of the subtropical zone and also are inhabitants of the littoral belt where temperature relations are complicated by the influence of air temperatures and considerable insolation at periods of low water. It may be for these reasons that these two species also extend into the Lower Boreal Zone as is indicated by some statements as to their distribution. Two other of the two-zoned species are mud and shallow-water species and probably are normally subtropical, extending over into spots in the temperate zone where the combination of shallow quiet waters and higher air temperature allows the air and the sun to raise the temperature of the water some 5° C. or even more, for a sufficient length of time each season or, at least in an occasional season of fairly frequent occurrence. The two species just referred to are *Zostera nana* Roth and *Z. pacifica* S. Watson. It may also be mentioned here that it is by no means sufficiently certain as to the exact limits of the distribution of either of these two species. The fifth species of this two-zoned group is *Cymodocea antarctica* (Labill.) Endl. This species occurs on the western as well as on the southern coasts of Australia and on the northern shores of Tasmania. This seems likely, for similar reasons to those advanced in the case of *Zostera capricorni*, to be a case of seasonal invasion of the South Subtropical Zone from the South Temperate Zone. It may be, however, an invasion in just the opposite direction, viz., from the South Subtropical to the South Temperate Zone, since according to Tepper (1881) the South Temperate plants increase only by a peculiar and specialized vegetative splitting off of buds or short branchlets.

The cases of species credited to three or more zones are more complex if we undertake to show that, in spite of this extended distribution, they are to be regarded as steno- rather than eurythermal. There are two of these, at least at present, considered to be of very extensive distribution, viz., *Halophila ovalis* (R. Br.) Hook. f. and *Zostera marina* L. The first seems to center in the

tropics of the Red Sea, the Indian Ocean and the tropical portions of the western Pacific. It extends also around Australia and to the northern portion, at least, of Tasmania. The second species is more characteristic of the northern hemisphere, extending southward from the arctic regions to the tropics both on coasts of the Atlantic and the Pacific. The second species, however, seems to be rare in both the tropics and in the frigid zones and probably has its center of distribution in one or other of the intermediate zones. It seems best to examine the facts concerning both of these species in some detail.

The first species of this really extensive distribution to be considered is *Halophila ovalis* (R. Br.) Hook. f., which is generally credited with being widely distributed through the tropical portions of the Red Sea, Indian and Pacific Oceans. It also extends entirely around the continent of Australia and occurs on the shores of Tasmania touched by Bass Strait. The extensive distribution in the tropical waters seems to mark this species as normal to the Tropical Zone, although it may be questioned as to whether one or more species are included, even here, under the name, since in 1909, Ostenfeld separated the plant of the Marianne and Philippine Islands as a separate species under the name of *Halophila ovata* Gaud. If the determinations are correct, however the occurrence of *H. ovalis* on the coasts of Australia extends the distribution through the South Subtropical into the upper portion of the South Temperate Zone. This would mean the endurance of temperatures from at least 18° or 19° C. upwards to about 29° C. It is manifestly impossible to do more than to discuss a case like this and to suggest possibilities as to how a species, whose lower limit of temperature persistence may be supposed to be 25° C., may exist in localities where the mean maximum is indicated as about 18° C. or at most 19° C. There are, however, several possibilities which might be investigated by those having an opportunity of studying the living plants. In the first place, the plants of the Australian and Tasmanian coasts are sterile, or, at least, have not been found in other than vegetative condition. It may be that the plants of these countries are of a different species from those of the tropics. In opposition to this, it may be said that Ostenfeld credits this species, with which he is presum-

able familiar, to the coast of Western Australia as late as 1916. His plants, however, were sterile. In the second place, this matter of the sterility of the Australian and Tasmanian specimens which seems to be the general testimony from Bentham in 1878 (vol. 7, p. 183) on to Ostenfeld in 1916, may indicate that this southern extension of the range is composed of plants which never fruit and which possibly increase in number and, therefore persist, through vegetative multiplication only. Unfortunately, there is too little information as the habits and methods of dispersal of this species, but it is extremely likely that vegetative methods of propagation may be important in the establishment and persistence of this species. The third and possibly the most probable alternative is that the shallow cooler waters inhabited by plants of this species, may through the higher temperature of the air and through insolation be raised six or eight or even more degrees in temperature for a sufficient number of days or weeks to enable the plants to flower and to ripen their seeds. This amount of increase of the temperature of shallow protected waters is known to occur. While no one of these three possibilities can be demonstrated to be actually in operation, yet there seems to be sufficient reason for not regarding the extensive distribution of this species as indicating a eurythermal character so far as persistence through seed-reproduction is concerned. That the species in general is eurythermal, may be granted, since the sum total of its endurance extends over a greater interval than 5° C. or even 10° C. We may suspect, however that there is very little vital activity during the lower periods of temperature experienced, but the ability to withstand such lower temperatures in a condition of quiescence or rigor. In other words, such a seeming eurythermal species as this probably is able to endure a period of hibernation while the other strictly tropical species of *Halophila* are not. A second assumption in the case of *Halophila ovalis* is that it is a perennial species, as its whole appearance and general structure indicate.

The second and other species of marine spermatophyte credited with extensive distribution is the common eel-grass or grass-wrack, *Zostera marina* L., of the northern hemisphere. The distribution of this species, as generally given, extends from high north (at least Lower Boreal Zone) to well within the Tropical

Zone (Florida and the Riu-Kiu Islands). This is certainly a perennial species and one capable of wide dispersal. It seems to be readily dislodged from the sand or mud in which its rhizomes are buried and floats long distances because of the gases contained within the numerous air-passages within its leaves. There is good reason, also, for suspecting that two, or even three, distinct genetic entities are included under this specific name, if not at least two distinct taxonomic species. The typical *Zostera marina* is generally considered to be the flat- and broad-leaved form while a variety with somewhat shorter, narrower and thicker leaves is called var. *angustifolia* Hornemann. There seems also to be a form intermediate between the two and this corresponds, in part at least, to f. *stenophylla* Aschers. & Graebner. The species and var. *angustifolia* often occur together, but apparently always separated according to substratum and somewhat possibly according to depth, the variety in a belt above that occupied by the species and restricted to a firmer substratum. Ostenfeld, in 1908, made a series of studies and careful measurements of these various forms and came to the conclusion that the differences were the results of more favorable *vs.* less favorable environment. I am inclined to suspect, nevertheless, that there are at least two genetically distinct varieties, or even species, which overlap in their distribution, the narrow-leaved variety preferring shallower water and firmer substratum than the broader-leaved form (or forms) and being able to extend farther into the areas of colder waters than the broader-leaved forms. Very little seems to have been done as yet as to the collection and study of the flowers and fruits, and especially of ripe seeds, at various localities in the range and this leaves much to be desired especially as regards seasonal data.

On the coasts of Europe, *Zostera marina*, in one form or another, has been given a range from Iceland and the extreme north of Europe to and including the Mediterranean Sea, but, as near as I am able to determine, the extreme northern locality, viz., White Island in the Kara Sea is based on the report of a non-botanist (cf. Ascherson, 1906, p. 402). It seems to stop, so far as general and continuous distribution is concerned, at Tromsoe, Norway, or somewhat below, but does occur in the Varanger Fiord and in Porsanger Fiord and in the White Sea on the northern coast of

Europe. These northern plants seem to belong to var. *angustifolia* (cf. Blytt, 1861, p. 1278). *Zostera marina*, in the extended sense seems to be fairly continuous along the western coast of Europe down to the neighborhood of Cadiz in Spain, while in the Mediterranean Sea it is less common and of spot-wise occurrence. It occupies, therefore, so far as the European coast is concerned, the Lower Boreal and North Temperate Zones without question and probably also extends discontinuously into the Upper Boreal and the North Subtropical Zones.

On the eastern coast of Asia, *Zostera marina* extends from somewhere near the Bering Strait south to and including some of the Riu-Kiu (or Loo Choo) Islands, thus occupying the Upper and Lower Boreal, the North Temperate, the North Subtropical and the upper portion of the Tropical Zones. I am unable to find out very much concerning the details of distribution on the Asiatic coasts. The relation of *Z. japonica* Aschers. & Graebner (1907, p. 32) to cited references is not clear. Turning to the eastern coasts of the North Pacific Ocean, it is reported from Port Clarence, Alaska, and from various localities along the coast south to Catalina Island, California, thus occupying the Upper Boreal, Lower Boreal, North Temperate, and possibly also entering the North Subtropical Zones. [*Z. oregona* S. Watson is not recognized by Ascherson and Graebner, but is referred to *Z. marina* (cf. Ascherson, 1906, p. 402).]

The data as to the distribution of *Zostera marina* along the eastern coast of North America are the most extensive and exact of any immediately accessible to me and, consequently, I shall lay more stress upon them. They are, however, by no means sufficiently comprehensive to form a satisfactory basis for an opinion, as I shall attempt to indicate. There is little doubt but that some form of it has been found in the inner portion of Pisigsarfix Fiord, at lat. 64° 35′ N. on the coast of southwestern Greenland (cf. Lange, 1887, p. 282). The species and its variety *angustifolia* reappear at the Strait of Belle Isle, no records being available of its occurrence on the intervening coast of Labrador. It is evidently abundant in the Gulf of St. Lawrence and along the coast of New England to New York Harbor. There is plenty of specimens to show the distribution from Newfoundland

to New York divided between the Gray Herbarium and that of the New York Botanical Garden. The specimens of the southern portion of this part of the range are largely, although not entirely the broader form of the species. Both Britton (1881, p. 100 and 1889, p. 259) and Stone (1911, p. 166) say that it is common in all bays along the coast of New Jersey, although the latter adds that it has not been found on the New Jersey shore of Delaware Bay. Stone also states (*loc. cit.*) that it has been observed in flower and fruit only in June and this is confirmed in a letter from Bayard Long, while above Cape Cod it is in fruit in August. I have not found a specimen in either the Gray Herbarium or that of the New York Botanical Garden from any part of our eastern coast south of New York Harbor. It is reported as frequent in shallow water in Chincoteague and Chesapeake Bays on the coast of Maryland by Shreve, Chrysler, Blodgett and Besley (1911, p. 395), and there is certain report of it as growing in abundance on the northern stretch of the coast of North Carolina. The only locality reported south of North Carolina is that of West Florida. This was made by Chapman (1860, p. 444) and repeated by Small (1913, p. 41), but I can find no specimen to verify it. Ascherson, in his later paper on the distribution of the "sea-grasses" (1906, pp. 401, 402) suggests that the Florida plant was probably some other species of this group. Temperature conditions favor West Florida as a possible locality for its growth. In his Flora of Bermuda, Britton (1918, p. 6) designates *Zostera marina* as a "native" plant, but the only specimen preserved in the herbarium of the New York Botanical Garden and labelled as from Bermuda consists of entangled leaves evidently cast ashore, but is supposed to have come from nearby shoals. It is to be noted that this specimen is plainly of the broad-leaved typical form of the species. It does not seem to occur in the Bahama Islands.

In attempting to deduce from the data of distribution as I have outlined them, the true conditions and laws of distribution of *Zostera marina*, there are certain considerations which stand out as of importance. I shall divide them under six heads, as follows:

(1) *Zostera marina*, as estimated taxonomically, probably consists of two or more genetic entities which seem to have

slightly different temperature relations, the narrow-leaved forms extending farther north than the broader-leaved forms;

(2) all forms of *Zostera marina* occupy shallow water in protected bays or inlets and, consequently inhabit the warmer waters of the zone or province they inhabit;

(3) it seems most probable to assume that the North Temperate Zone is the normal zone for *Zostera marina*, since a comparison of the distribution on all coasts indicates this zone rather than the North Subtropical or the Lower Boreal, the other two zones in which it is widespread;

(4) the southward invasion from the North Temperate Zone into the North Subtropical is not extensive on either the west coast of Europe or on the west coast of North America, but is extensive on the east coast of North America and on the east coast of Asia. The suggestion naturally is that these latter extensions are due to the greater deflections of the colder waters, as indicated by the lines of mean minima, on these coasts, *i.e.*, are seasonal invasions, e.g., chart 266 of B. M. Davis (1913, p. 536) indicates that *Z. marina* is an invader from colder waters at Woods Hole, Massachusetts;

(5) the invasions northward from the North Temperate Zone into the Boreal Zones are probably due to the localities, seemingly always situated at the innermost portions of long fiords, being raised in temperature (cf. Kjellman, 1883, p. 31) by the air temperature and by insolation;

(6) it may also be urged that the capacity of *Zostera marina* to continue its occupation of a particular locality and to spread to other even far distant localities, through its adaptions for floating and vegetative multiplication, may have some bearing on the extensive distribution of this species (cf. Ascherson, 1906, p. 402).

In conclusion, it may be well to summarize the principal points of general interest brought out or suggested, in the consideration of the marine spermatophytes.

1. The marine spermatophytes are largely made up of plants surrounded by a medium whose temperature at any given time is the same for all parts of the plant. The species of *Phyllospadix* alone present to a certain extent, at least, the temperature con-

ditions of terrestrial spermatophytes in that, at periods of low water, they have their roots in soil (or sand) of one temperature and their leaves in air of another. The majority of the marine spermatophytes live under a greater uniformity of temperature conditions than do the terrestrial spermatophytes.

2. The marine spermatophytes live under conditions very similar to those experienced by the marine algae and show the same temperature-zone relations as the marine algae.

3. The great majority of the species of the marine spermatophytes are confined strictly to one temperature zone of 5° C. amplitude of the monthly mean maximum of the surface waters. Such species are strictly stenothermal from every point of view and may be supposed to represent the normal type in distribution.

4. There are certain species which extend over two zones of temperature. It seems possible in these cases, as it has also seemed possible in the cases of certain marine algae, to regard these marine spermatophytes as normal to one zone whence they invade the other because they find in certain localities of the invaded zone their proper temperature, both as to intensity and duration. The invasions of the marine spermatophytes, like those of the marine algae, proceed in two directions in the cases of the two-zoned species, viz., from a warmer into a colder zone because of the existence of warmer spots among the colder areas normal to the zone, or from a colder into a warmer zone because of a seasonal lowering of the temperature of the warmer zone or portions of it.

5. There are a few species which are credited to more than two temperature zones and such are also found among the marine algae. It may be that these species being normal to one temperature zone, may invade not only one zone, but two or more additional zones because of the existence of localities or seasons of suitable temperature. This movement may be in only one direction from the normal zone, as in the case of *Halophila ovalis*, or it may be in two directions from the normal zone, as seems to be the case with *Zostera marina*.

6. Finally attention may be called to the difficulties attending the study of the distribution of a species caused by the incompleteness of our knowledge of its homogeneity or the lack of it,

its persistence through one or more seasons, its dependence upon spore reproduction or its ability to persist through vegetative multiplication, its seasons of flowering, fruiting, etc., in different portions of its range, any difference in habitat in different portions of its range, and any other matters which may be characteristic of the behavior of the species and which may possibly vary according to locality. The case of *Zostera marina* certainly indicates how much it is desirable to increase our knowledge of such species before we may feel certain that we are in any advantageous position to discuss the factors concerned in their very extensive distribution.

UNIVERSITY OF CALIFORNIA

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Notes on trees and shrubs of eastern North America

W. W. Ashe

PRUNUS ALLEGHENIENSIS Porter, Bot. Gaz. **2**: 85. 1877

The southern limit of this species in the most recent publication* in which its distribution is considered is given as central Pennsylvania, where it was originally discovered. It has been found to be locally abundant along the foot of the Blue Ridge in Rockbridge County, Virginia; on the slopes of the Great Shenandoah Mountain in Rockingham County, Virginia; and in Highland and Pendleton Counties, West Virginia. The fruit is locally used and highly prized for making a bright-colored and tart jelly.

In 1916 I collected near Georgetown, South Carolina, specimens and growing plants of an *Azalea* which was published under the name *A. atlantica* Ashe.† The flowers of this were described as pale rose-purple but they are really white or nearly so, becoming purplish as they wilt, the description having been drawn from wilted specimens. A careful study of additional material and of cultivated plants seems to show that there are two closely related species, the one, *A. atlantica*, with white flowers which change to pale rose as they wilt, and the other with rose-purple flowers. The latter is apparently undescribed and may be known as:

Azalea neglecta sp. nov.

A stoloniferous shrub forming small patches, the branches 1–3 dm. high. The fragrant flowers in compact clusters of four to ten, the corolla pale rose-colored with a reddish or purplish pubescent tube; lobes acuminate and very slightly viscid on the back are as long as or longer than the slender tube; stamens five, long-exserted, about the length of the lobes, style 4–5 cm. long. Twigs when young sparingly pubescent with short spreading hairs, becoming gray and glabrous the second season. Leaves 4–6 cm. long, narrowly obovate, mucronate and abruptly acute at apex, cuneate at the base, dark green above, pale and glaucescent beneath, pubescent on the midrib and ciliate on the margins.

* Britton, N. L. North American Trees, page 489. New York.

† Bull. Charleston Mus. **13**: 26. 1917.

Growing with *A. atlantica*, beneath *Pinus Taeda* and *P. serotina*, in low pine flat-woods, northeastern South Carolina and adjacent parts of North Carolina. Like *A. atlantica*, the species above proposed flowers before the leaves are fully grown, a character which separates these two plants from all forms of *A. viscosa*, with which they grow but which flower two months later. TYPE collected by W. W. Ashe in May, 1916, near Georgetown, South Carolina. Living plants from the original collection have since been cultivated. *A. atlantica* differs from this plant in having white flowers which become purplish as they wilt; a longer tube to the corolla; the tube glandular-viscid and also the backs of the lobes, which are shorter than the tube; and light green foliage, slightly pale but not glaucous beneath. The tube of the flower of *A. neglecta* is not viscid, and the rose-colored flowers have a shorter tube and longer, more slender lobes than those of *A. atlantica*.

AZALEA ARBORESCENS Pursh

Although this species occurs as far north as Pennsylvania it is regarded as a mountain species. What seems to be a dwarf form, however, has been found at Great Falls, Virginia, on the Potomac River, which adds it to the flora of Washington, D. C. It flowers freely there in early summer as a shrub less than 3 dm. high. Low flowering plants of this kind have never been noted for this species in the Appalachian Mountains where it is best developed.

INDEX TO AMERICAN BOTANICAL LITERATURE

1917–1920

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

This Index is reprinted monthly on cards, and furnished in this form to subscibers at the rate of two cents for each card. Selection of cards is not permitted; each subsciber must take all cards published during the term of his subscription. Correspondence relating to the card issue should be addressed to the Treasurer of the Torrey Botanical Club.

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